SEASONAL CHANGES IN BEHAVIOR AND EXHIBIT USE OF CAPTIVE AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*) AND BLACK RHINOCEROSES (*DICEROS BICORNIS*)

by

JENNI ELIZABETH MUELLER

Submitted in partial fulfillment of the requirements
For the Degree of Master of Science

Department of Biology
CASE WESTERN RESERVE UNIVERSITY

August, 2008

CASE WESTERN RESERVE UNIVERSITY
SCHOOL OF GRADUATE STUDIES

We hereby approve the thesis/dissertation of

____________________Jenni E. Mueller___________________

candidate for the _________Master of Science_________degree *.

(signed)__________Julia Brown____________________________
(chair of the committee)

__________Kristen E. Lukas_________________________

__________Mark A. Willis__________________________

__________Pam Dennis_____________________________

____

____

(date) ________June 26, 2008________

*We also certify that written approval has been obtained for any proprietary material contained therein.

Table of Contents

List of Tables

Introduction

Chapter 1

Chapter 3

List of Figures

Chapter 1 **Page No.**

Chapter 2

Chapter 3

Chapter 4

Seasonal Changes in Behavior and Exhibit Use of Captive African Elephants (*Loxodonta africana*) and Black Rhinoceroses (*Diceros bicornis*)

Abstract

by

JENNI ELIZABETH MUELLER

Despite living in the same habitat and sharing many physiologic characteristics, African elephants and black rhinoceroses are behaviorally very diverse. Each species therefore copes with the challenges of a captive environment in different ways. This study examined the behavior and exhibit use of three African elephants and three black rhinoceroses over a one-year period to determine how each species adapted its natural behavior to captivity in a northern climate. In both species, total time spent active was similar to that seen in the wild. Increased time housed indoors resulted in decreased investigatory behavior and increased abnormal behavior in elephants, and decreased locomotion in rhinos. Both species utilized all areas of the outdoor enclosures, but spent more time than expected near the Building and Door areas. Elephants also favored the Trees, while rhinos favored the Mud Wallow. Individual differences within each species were most prevalent in abnormal and social behaviors.

Introduction

Species-typical behavior patterns are shaped by evolution to correspond to the animal's physical, ecological, and social needs, forming behavioral repertoires that function specifically in that natural environment. Even within one species, however, different populations may encounter variations in environmental factors and hence species retain some ability to adapt their behavior as a method of coping with a given situation (Carlstead, 1996; Hutchins, 2006; Mason & Mendl, 1993). It is this adaptability and natural coping response that allows wild animals to be held successfully in captivity, as captive environments present new stimuli, expunge other stimuli and require an animal to adjust to an unnatural environment (Carlstead, 1996; Schulte, 2000). Not every individual or species can cope with every situation, however, as species and even individual differences in genetics, development, and previous experience can affect how an animal adapts to either barren or naturalistic captive environments (Carlstead, 1996; Freeman et al, 2004). Additionally, the more an individual is required to cope the more compromised its welfare may be (Veasey, 2006). One important aspect of zoo research is therefore determining whether an animal has successfully adapted to its captive environment, and a vital component of this adaptation is behavior.

Proper care in captivity requires evidence-based husbandry and management standards of environmental, social, and behavioral needs (Hutchins, 2006; Veasey, 2006). Natural conditions cannot be precisely recreated, but to determine what is sufficient necessitates research on captive animals. With large mammals especially, research requiring physiological measurements or experimental manipulations are not often feasible and hence behavior is an important aspect in determining well-being (Veasey, 2006). While some deviation from natural behavior is not necessarily problematic, ideally behavior in captivity should overall closely resemble that seen in the wild (Hutchins, 2006). Meeting the behavioral and biological needs of animals becomes especially important with intelligent and social species, as they are more psychologically vulnerable to improper environments (Douglas-Hamilton et al, 2006; Veasey, 2006). Many mammals have demonstrated degrees of intelligence and self-consciousness, and the ability to maintain competent societies additionally requires an understanding of the behaviors and intentions of conspecifics (Mench & Kreger, 1996; Veasey, 2006). Two species that have displayed both individual intelligence and intricate social behaviors are the African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*).

American Association of Zoos and Aquariums (AZA) institutions currently hold approximately 202 African elephants and 186 black rhinoceroses (Table 1) (International Species Information System, 2007).

Table 1: Captive Populations of African Elephant and Black Rhinoceros

	Worldwide	AZA Institutions
African Elephant (*L. africana*)	69.268	25.128
Black Rhinoceros (*D. bicornis*)	95.90	65.45

Data presented as [#males.#females]

[1]International Species Information System (2007)

Neither captive population is self-sustaining, and a major factor in improving husbandry and increasing birth and survival rates is behavioral research. For instance, behavioral studies can be used to determine the effect of management practices such as feeding and enrichment; to assess reproductive behavior and mating difficulties; and to evaluate mother-infant relationships (Foose & Wiese, 2006; Wiese & Willis, 2006). Multi-institutional studies on behavioral and health parameters have been conducted on both species (e.g. Brown et al, 2004; Carlstead et al, 1999a,b; Freeman et al, 2004). Although this research is necessary to provide a broad picture of the state of the captive population, it generally utilizes surveys to document behavior and therefore may be subjective and cannot give accurate assessments of activity budgets, social interactions, or changes due to environmental stimuli. Studies focused on a single group of animals at one institution lack the statistical power and large-scale extrapolation of multi-institutional studies, but are beneficial in that they allow for observational data collection and comparisons of different individuals or species within the same environment and under the same management system.

This study provides a longitudinal analysis of the behavior of three African elephants and three black rhinos housed at Cleveland Metroparks Zoo (CMZ). The purpose was to compare how two behaviorally distinct large ungulate species that evolved in similar natural habitats adapt their behavior to a captive environment, with an emphasis on solitary activity budgets and exhibit use, abnormal behaviors, social interactions and social hierarchies.

Natural History of the Species

African Elephants

During the first half of the twentieth century there were over one million wild African elephants, more than double the current population. During the late 1970's and early 1980's the largest drop in numbers occurred, because of an increase in poaching related to the ivory trade (Foley et al, 2001). Today the African elephant is considered a vulnerable species (African Elephant Specialist Group, 2004) and continues to be threatened by illegal poaching for ivory and bush meat, as well as habitat loss and human-elephant conflict. Together these factors have caused not only a decline in numbers but also fragmentation of the populations, leaving elephant populations in some areas of Africa severely diminished and in others so large as to necessitate culling (Foley et al, 2001).

African elephants live in matriarchal societies characterized by extensive social integration, including coordinated movements, cooperation among adults, and group care of calves (Schulte, 2000; Vidya & Sukumar, 2005). Wild herds average 10 to 12 individuals and consist of mostly related adult females and their offspring (Estes, 1991; Garai, 1992; Vidya & Sukumar, 2005). Subadult males leave their natal group between nine and 18 years of age (Vidya & Sukumar, 2005). They may form temporary, unstable bachelor groups when not in musth, but adult bulls are typically solitary and only associate with other elephants when mating (Buss, 1990; Spinage, 1994; Vidya & Sukumar, 2005). Females remain with their natal group through adulthood and it is rare for unrelated elephants to form permanent alliances or join established family groups. Families will, however, often engage in affiliative interactions when encountering other herds during travel (Schulte, 2000). These greeting ceremonies are initiated by the groups' respective matriarchs, or leaders, who are generally the oldest females in the herd. Matriarchs are crucial to the survival and success of these families because of their experience and extensive knowledge of the environment and available resources. This accumulated information is then transmitted through generations via learning (Freeman et al, 2004; Spinage, 1994; Vidya & Sukumar, 2005). The death of a matriarch is therefore a significant event, often resulting in group distress or splitting of the herd. Individuals from other family groups have been reported visiting recently deceased matriarchs (e.g. Douglas-Hamilton et al, 2006). Family units may also divide if the herd becomes too large or resources too scarce, but rarely do these smaller groups contain less than four or five individuals (Schulte, 2000).

African elephants are long-lived and inhabit a dynamic environment. By maintaining these strong social bonds elephants garner both immediate and delayed benefits that enhance survival, including predator defense and knowledge of resources (Archie et al, 2006; Schulte, 2000; Vidya & Sukumar, 2005). However, the major factor in the evolution of elephant sociality was likely offspring care (Schulte, 2000). Calves provide a way for younger females to practice mothering skills and also strengthen group cooperation skills via the necessity of predator defense (Schulte, 2000). Elephants thus have a powerful familial relationship, and many researchers believe that this has developed into a generalized interest in both related and unrelated conspecifics (Douglas-Hamilton et al, 2006; Schulte, 2000). A social system built upon both lifelong bonds within a family group and between family groups in a population necessitates behavioral flexibility and the ability to identify others and evaluate the nature of their behaviors (Garai, 1992; Wittemyer & Getz, 2007). This ability highlights the elephant's cognitive capacities.

Central to the African elephant's social structure is multisensory communication. Elephants cannot see far away but are sensitive to movements, and visual signals utilize this sensitivity by relying upon movement of the head, ears, trunk, and/or body (Langbauer, 2000; Spinage, 1994). Visual communication is especially important in aggressive interactions, as impressive displays often preclude potentially deadly fights (Spinage, 1994). Visual displays are also common in greeting ceremonies, mating behaviors, and play (Vidya & Sukumar, 2005). Tactile communication using either the trunk or body is associated with affiliative, explorative, sexual, and playful interactions and is also thought able to provide reassurance during stress (Estes, 1991; Vidya & Sukumar, 2005). Olfaction and taste combine to provide a highly sophisticated chemosensory system consisting of the trunk and vomeronasal organ; chemical cues are used to indicate physiological condition (i.e. estrus or musth), for individual recognition, and for group cohesiveness (Langbauer, 2000; Vidya & Sukumar, 2005).

Acoustic communication is perhaps the most studied of the elephant's systems. The acoustic repertoire of elephants ranges from 10-9000 Hz, with typical calls between 14-24 Hz and up to 100 dB (Spinage, 1994; Vidya & Sukumar, 2005). They also use infrasound, or seismic calls that can be felt through the ground and often cannot be heard by humans; these calls can travel up to five km (Langbauer, 2000; Vidya & Sukumar, 2005). The pitch, volume, and duration of a call combine to relate a specific message regarding an immediate situation (Estes, 1991; Langbauer, 2000). Calls are rarely unanswered and it is believed that elephants can use the harmonic attenuation of a call to determine the direction and distance to the source (Langbauer, 2000). Acoustic communication is used over both short and long distances for communication within and between family groups, and serves many functions such as greetings, mating calls, locating individuals, and avoidance (Langbauer, 2000; Spinage, 1994). Each individual has a distinct "voice," and it is believed that unintended receivers listen to calls as a way of learning other group's vocalizations (Estes, 1991; Vidya & Sukumar, 2005).

Humans are the only major threat to wild African elephant populations, as adults have no natural predators and the species can exist in nearly any habitat that provides ample food and water resources (Estes, 1991). They can spend up to 18 hours per day feeding and during that time ingest approximately 5% of their body weight. Their inefficient digestion results in less than half of this being converted into energy (Estes, 1991; Spinage, 1994). Elephants browse on a much larger selection of plants than most other herbivores (e.g., leaves, twigs, bark, root, seeds, and flowers), and utilize mineral licks for additional nutrients (Estes, 1991; Stoinski et al, 2000). The distribution of food and other resources is the primary factor in determining home range size of female herds, with poorer conditions resulting in more movement and larger ranges (Ntumi et al, 2005; Spinage, 1994). Home range sizes therefore can vary both by location and by season, as dry weather forces elephants to roam farther in search of adequate food; in the wild home range sizes between 30 and over 7000 km^2 have been reported (Ntumi et al, 2005). Solitary bulls base their range on the availability and movement of the females; home ranges of multiple female herds and/or males generally overlap (Spinage, 1994). This fluid spatial pattern is aided by the fact that African elephants are not territorial, which provides decreased intergroup aggression and increased movement availability (Buss, 1990). It also allows elephants to share their habitat and resources with numerous other ungulate species, one of which is the black rhinoceros.

Black Rhinoceros

The black rhinoceros, which once was found throughout most of sub-Saharan Africa, currently ranges through the semi-desert and bushland areas

(Garnier et al, 1998; Hutchins & Kreger, 2006) and is listed as Critically Endangered by the World Conservation Union (African Rhino Specialist Group, 2003b). As with the elephant, the primary danger to the black rhino is human interference, including poaching and habitat loss due to human encroachment. Rhino horns have long been sought after for medicinal and decorative purposes, and logging, agriculture, and increasing human settlement have resulted in significant habitat loss. Together these anthropogenic threats led to an over 95% population decrease between 1970 and 1992 and left fewer than 2500 black rhinos in the wild (Hutchins & Kreger, 2006). Conservation efforts and international trade bans helped to boost the population to approximately 3100 animals in 2001 (African Rhino Specialist Group, 2003b). Most wild populations are managed in protected areas, but these tend to be small and isolated and habitat loss, illegal poaching, and lack of genetic diversity are still a threat to the species (Garnier et al, 1998; Garnier et al, 2002; Patton et al, 1999). Proper management of both wild and captive black rhinos is therefore imperative to increase the population (Hutchins & Kreger, 2006). One goal in this effort is a more complete understanding of rhino biology and behavior (Hutchins & Kreger, 2006; Patton et al, 1999).

Black rhinos are browsers, feeding on over 200 species of shrubs, herbs, and small trees found at the forest periphery (Benyus, 1992; Estes, 1991); they have no incisors, instead using their prehensile upper lip to grasp food items and pull them into the mouth (Estes, 1991). They eat many of the same plant species as African elephants and even rely upon elephants to open browsing areas along the edge of the savannah (Schenkel & Schenkel-Hulliger, 1969). Their typical food sources are considered low-quality, and along with an inefficient digestive system require the rhino to eat large amounts of food daily. They are therefore opportunistic feeders similar to elephants, and as such home range size depends mostly on resource distribution. Reported home ranges vary from less than three to over 500 km^2 (Hutchins & Kreger, 2006). Males tend to have larger home ranges than females, and sub-adults larger than adults (Estes, 1991). Home ranges of different individuals often overlap, and typically include movement trails, scent posts, and dung piles utilized by individuals of both sexes in the area (Estes, 1991).

Black rhinos are not considered territorial, but will use scent marks (urine and feces) throughout their home ranges to denote their position and movement pattern. As this species is solitary and relies greatly on its sense of smell these markings are integral in providing a means of indirect communication within the population: unlike acoustic and visual signals, scent marks can last for days and the initiator need not be present when the signal is received (Benyus, 1992; Schenkel & Schenkel-Hulliger, 1969). Black rhinos are thought to use fecal marks for individual identification, and urine marks for space and activity regulation (Estes, 1991; Hutchins & Kreger, 2006; Kretzschmar, 2002; Schenkel & Schenkel-Hulliger, 1969). When conspecifics interact at close range rhinos will also use vocalizations and visual displays, though to a much lesser extent then the elephant. Interactions between a calf and cow or mating male and female will often include vocalizations, as will agonistic interactions between males and/or females (Estes, 1991). Visual communication is mostly associated with agonistic encounters and includes such displays as head tossing, side presentations, and mock charges (Benyus, 1992). As in elephants, these aid in preventing intense and possibly dangerous confrontations. Physical aggression between females is rare, and although male-male aggression is more common it is still not often seen (Schenkel & Schenkel-Hulliger, 1969).

The lack of natural predators has left rhinos with no avoidance techniques when threatened, save for running (Schenkel & Schenkel-Hulliger, 1969). Black rhinos are known for their heightened alarm response to humans, which is more acute than that shown by other rhino species. Individuals have been reported to run several hundred meters after detecting human scent or hearing alarm calls from other ungulates or even oxpeckers (Hutchins & Kreger, 2006; Schenkel & Schenkel-Hulliger, 1969). Although they have relatively poor vision rhinos can detect movement up to 60 m away and often their alarm response is lessened when the perceived threat can be detected visually. Schenkel and Schenkel-Hulliger (1969) found that seeing a human at 50 m caused most black rhinos to do little more than briefly orient in that direction. There is, however, considerable variation and unpredictability in responses to humans, including ignoring, investigating, and even charging. An individual's response depends on factors such as age, sex, locality and type of threat, temperament and past experience (Hutchins & Kreger, 2006; Schenkel & Schenkel-Hulliger, 1969).

African species of rhino are considered more gregarious than the Asian species, but black rhinos are generally solitary as adults (Hutchins & Kreger, 2006). Even courtship and mating behaviors in this species are brief, with the interaction between male and female lasting less than one hour (Schenkel & Schenkel-Hulliger, 1969). The relationships between cows and calves are usually the only stable bonds black rhinos form; subadults typically leave their dam when she is near parturition with her next calf (Hutchins & Kreger, 2006; Schenkel & Schenkel-Hulliger, 1969). Adult females calve every two to five years in the wild and have a gestation period of 15 months (Garnier et al, 1998); maturation does not occur until approximately seven years of age for females and ten years for males (Estes, 1991). As with the elephant, factors such as long gestations and slow maturation result in a slow increase in population numbers. Additionally, birth rates in the wild are not easy to determine (Garnier et al, 1998), making it difficult to determine accurate population numbers and project future growth.

Despite not being as dependent on conspecifics as group-living ungulates black rhinos frequently take notice of and even briefly interact with one another (Benyus, 1992; Schenkel & Schenkel-Hulliger, 1969). Congregations of up to five adult and/or sub-adult females have been reported but are generally unstable and temporary (Benyus, 1992; Estes, 1991; Hutchins & Kreger, 2006). Black rhinos may also associate at scarce resources such as water holes and mud wallows; these interactions tend to be tense but amicable (Estes, 1991; Schenkel & Schenkel-Hulliger, 1969). Schenkel and Schenkel-Hulliger (1969) noted a mud wallow being used by up to four rhinos; all stood at the approach of a new rhino and maintained personal spaces of approximately two meters, highlighting the apparent necessity of maintaining social distance. The authors also described female-calf pairs greeting and sniffing each other when passing on commonly used trails (Schenkel and Schenkel-Hulliger, 1969). Observations such as these also show that, despite being a solitary species, black rhinos will tolerate conspecific companionship and do maintain some social relations in the wild, if only to share habitats and resources. Although the social structure of this species varies greatly from that of African elephants, sociality itself remains an important aspect of black rhinoceros behavior.

Social Behavior

Social behavior in mammals is governed by two types of relationships: 1) Bonding relationships, which consist mostly of affiliative interactions; 2) Dominant relationships, which are established and maintained with agonistic interactions and determine social status (Sachser et al, 1998). Social bonds are reflected in proximity and affiliative interactions and help contribute to group stability, especially among mature adults (Heitor et al, 2006b). Dominant relationships are generally formed as a result of resource competition, such as for food, mates, or objects. These relationships vary in degree of despotism, nepotism, and tolerance and the balance between these elements determines how the relationship is behaviorally expressed (Wittemyer & Getz, 2007). Agonistic behaviors such as aggression, defense, and subordination are a primary feature of dominance relationships, and only rarely do these escalate into life-threatening fights (Koontz & Roush, 1996; Wittemyer & Getz, 2007). The presence of a bonding partner and degree of agonism within the group both influence the positive and negative aspects of a social environment (Sachser, 1998).

Stable social groups are less stressful than unstable groups, as they result in predictable behaviors from all individuals and reduced aggression (Heitor et al, 2006a; Sachser et al, 1998). Many species sustain stability through dominance hierarchies, or social systems consisting of dominance relationships between all pairs of individuals (Chase et al, 2002; Holand et al, 2004). Hierarchies can be linear or non-linear; linear hierarchies are always transitive, meaning each animal is dominant to the individual immediately subordinate to it as well as all the individuals subordinate to that individual (Archie et al, 2006; Chase et al, 2002). Depending on the species, hierarchical rank can be influenced by characteristics ranging from aggressiveness to height to matrilineal ranks, and established dominance relationships are rarely challenged (Chase et al, 2002; Heitor et al, 2006a). Winner-loser analyses of agonistic interactions are a traditional method of determining rank order among a group of animals, but in ungulates aggression is often seen in both offensive and defensive manners and subtler behaviors such as threats and avoidance are more common in established groups (van Dierendonck et al, 1995). This makes it difficult to rely solely on agonistic interactions to determine rank order. van Dierendonck et al (1995) found that in horses, which have no ritualistic dominance signals, subordinates are more likely to avoid dominant individuals (therefore avoiding possible aggression) because of the inability to acknowledge the other's dominance status if confronted. Avoidance was therefore a more reliable indicator of a dominant relationship than aggression (van Dierendonck et al, 1995), and subordinates are largely responsible for both establishing hierarchies and maintaining low levels of aggression within stable groups (Heitor et al, 2006a; Mikulica, 1991). Hierarchical ranks in other ungulate species may therefore be easier to resolve using avoidance behaviors and subordinate displays rather than overt aggression.

Female ungulates, including African elephants and black rhinos, generally exploit dispersed and relatively undefendable food sources (Holand et al, 2004). However, unlike many female ungulates both African elephants and black rhinos possess armaments typically only seen on males and also depend upon some rare and usurpable resources such as mineral deposits, wallows, and rubbing posts (Archie et al, 2006). Recent research on wild African elephants has suggested that herds have transitive linear hierarchies where dominance is primarily based on age (Archie et al, 2006). Wittemyer & Getz (2007) found that dominance relationships between groups were also transitive and rank was largely a factor of matriarchal age. Agonistic encounters between the groups were rare, suggesting established dominant relationships are remembered and respected; only a species with highly developed cognitive abilities could maintain this type of social order (Wittemyer & Getz, 2007).

Housing captive animals in unnatural social situations such as isolation and overcrowding has been linked to increased stress, stereotypies, and abnormal social behavior in zoo animals (Price & Stoinski, 2007). Even though many of the environmental factors necessitating group living in the wild are not present in captivity, species such as the African elephant that have evolved as social animals have a behavioral need for conspecific companionship. Solitary species such as the black rhino do not require the presence of other individuals but are often kept in social environments. Research on the sociality of both species will therefore be beneficial in captive management, and housing either species in captivity should be based upon its natural social structures and needs and take into account both group size and compatibility (Price & Stoinski, 2007). Research on the social behavior and dominance structure of captive groups is essential in determining appropriate social groupings and learning how both naturally social and solitary species adapt to the forced sociality of captivity. Additionally, captive environments provide the ability to witness rare social events and give a closer view of conspecific interaction than can usually not be seen in the wild (Koontz & Roush, 1996).

African Elephants and Black Rhinoceroses in Captivity

African Elephants

African elephants have been in captivity in North America for over 200 years (Schulte, 2000) and have always been considered a flagship species in zoos because of their size, intelligence, and public appeal (Vidya & Sukumar, 2005). They have a diverse behavioral repertoire, which contributes to public interest and to their ability to adapt to varied habitats. Captivity, however, imparts upon this species multiple environmental parameters that eliminate the need for many natural behaviors and/or make them difficult to perform (Veasey, 2006). Diets typically consist of grass or legume hay and concentrated pellets given in large spatially concentrated amounts, reducing the need for foraging and locomotory behaviors (Stoinski et al, 2000; Wiedenmayer, 1998). Captive enclosures are small and static as compared to the expansive, complex savannah habitats of Africa, and elephants housed in zoos in northern climates typically remain in indoor facilities throughout much of the winter. These small enclosures often have hard substrates and are associated with husbandry practices such as chaining and too little exercise, all of which have been blamed for health problems including arthritis, obesity, and foot troubles (Hutchins, 2006; Lemonick, 2006; Veasey, 2006).

The altered physical environment of captivity is considered a primary factor behind multiple health and behavioral problems in elephants, but the social environment has a strong impact as well. Unlike in the wild, captive social groups are typically small and composed of unrelated females (Hutchins, 2006; Olson & Wiese, 2000). Herds cannot interact with other herds and rarely have the chance to interact with males (Schulte, 2000). Furthermore, most females are not exposed to calves, which are an important source of group cohesion and activity in the wild (Hutchins, 2006; Schulte, 2000). Young captive females are unable to learn and practice mothering skills, which may be detrimental to their own success as mothers if they are later bred (Hutchins, 2006). Small groups and a static habitat may also negate the need for a true matriarch, further altering the species-typical sociality (Schulte, 2000). Captive female elephants also have low conception and birth rates, and because of this the captive population is currently not self-sustaining (Schulte, 2000). Less than 10% of reproductive-aged females have produced offspring, and approximately 30% of females show irregular ovarian activity or are acyclic, a condition that has been associated with behavioral abnormalities in other mammal species (Brown et al, 2004; Freeman et al, 2004). Acyclicity, or ovarian inactivity, is characterized by low and stable concentrations of serum progestins. This has been associated with a number of factors including nutritional deficiencies, reproductive tract pathology, disruptions of the hypothalamic-pituitary axis, and stress (Brown et al, 2004). The exact cause likely varies between individuals, making it difficult to diagnose and treat.

Brown et al (2004) analyzed serum samples from both cycling and non-cycling African and Asian elephants and suggested that environmental and social stressors may be a associated with acyclicity. Freeman et al (2004) found that acyclic females were more likely to be dominant and more disciplinary within their group and suggested that the biological malfunctioning could be the result of lack of behavioral control. Dominant females in captivity are not true matriarchs and may expend excessive energy reacting to the environment and protecting or disciplining other elephants; captive groups therefore do not often have the stable relationships typical of wild family groups (Freeman et al, 2004). Research on the social behavior and dominance structure of captive elephants will help determine how groups can best be managed to encourage natural social behaviors and stability.

Members of the animal behavior and AZA communities have expressed opposition to the continued exhibition of elephants because of the species' overall poor health and reproduction, stating that the numerous biological and behavioral problems associated with captivity are a testament to the inability of humans to properly house them in captivity (e.g., Lemonick, 2006). This has led multiple AZA institutions, such as Detroit Zoo, Bronx Zoo, and Philadelphia Zoo, to phase out elephant exhibits. Yet many others are countering this by redesigning current elephant exhibits or building new enclosures. Elephant management in captivity is clearly challenging, and this in part is because of a lack of knowledge of affecting factors such as disease, reproductive deficiencies, and behavior (Veasey, 2006). Noninvasive hormonal analyses of wild populations have suggested that environmental and human disturbances can reduce elephant reproductive success (Foley et al, 2001). Successful captive propagation of this species may therefore rely upon on the minimization of unnatural stressors, and additional research is necessary to further clarify how social, environmental, and managerial variables of captivity affect the biology and behavior of African elephants (Schulte, 2000).

Black Rhinoceros

Captive black rhinos are not a self-sustaining population, and the need to reach the desired carrying capacity without the addition of animals from the wild means determining what factors are affecting captive population growth (Smith & Read, 1992). Captive research is not as prevalent with this species as with African elephants, and little work is done in behavior. Currently studies on health and reproductive biology are emphasized; black rhinos have high disease and mortality rates (Carlstead et al, 1999b), and females have inter-birth intervals and shorter reproductive life spans than wild rhinos. Furthermore, nearly one-third of females fail to breed in captivity (Carlstead et al, 1999a; Smith & Read, 1992). Much research is therefore focused on reproductive physiology in an effort to determine how to increase population levels. Pregnancy detection in black rhinos through the use of fecal progesterone metabolites was confirmed by Berkeley et al (1997). Brown et al (2001) were the first to compare yearly fecal hormone profiles in captive black and white rhinos. Their cross-institutional study measured both reproductive and stress hormones and suggested that the reproductive problems associated with black rhinos are not the result of ovarian dysfunction: 39% of females had cycle lengths outside of the average 20-32-day range, but most did cycle once per month throughout the year. The difficulties associated with captive breeding and conceiving may therefore not be purely physiological, but instead possible results of social and environmental factors. Corticoids, or stress hormones, were not correlated with reproductive hormone patterns, but that does not necessarily mean stress does not affect reproduction. Corticoids were approximately 30% higher in black rhinos than white rhinos; this effect may be linked to species or population differences, but may also be because of increased susceptibility to stress in black rhinos (Brown et al, 2001).

Chronic stress has been associated with reproductive deficiencies and decreased immunological responses in many animals (Lane, 2006), and the captive black rhino population has both low reproductive rates and high rates of disease. The response of a rhinoceros to a stressor is dependent upon individual characteristics such as temperament and past experience, as well as how the stressor is perceived and what response options are available (Brown et al, 2001; Carlstead et al, 1999a; Carlstead et al, 1999b; Schenkel & Schenkel-Hulliger, 1969). Captivity presents multiple environmental challenges to this species similar to those seen with elephants: enclosures do not often reflect the large and diverse habitat typical of wild home ranges; management practices that rely upon scheduled feedings of hay and pellet feeds prevent natural foraging behaviors; and individuals have fewer locomotory opportunities and needs (Hutchins & Kreger, 2006). Whereas elephants are typically housed in unnaturally small herds, solitary black rhinos are often kept in pairs or small groups that would not be seen in the wild (Hutchins & Kreger, 2006). However, just as with elephants, compatibility may be more important than strictly natural groupings: while some rhinos are aggressive or fearful around conspecifics, some have been successfully housed in social groups. Individual differences within this species clearly affect behavior, emphasizing the need for further quantitative studies of exhibit use, solitary activity, and social interactions with multiple rhinos at multiple institutions. This research can potentially clarify how behavior, health, and reproduction are affected by the physical and social environments of captivity (Carlstead et al, 1999a; Mills, 1997; Swaisgood et al, 2006).

Abnormal Behavior

Abnormal behaviors include behaviors and behavioral patterns not typically seen in the wild and have long been considered the product of poor welfare (Mason, 1991; Mason et al, 2007; Veasey, 2006). Though not necessarily maladaptive, which implies a pathological condition and/or high cost of performance, they are undesirable in captive facilities because of their negative appearance and are often accompanied by a progressively diminishing natural behavioral repertoire (Dantzer, 1986; Mason, 1991). Most are characterized by a repeated, invariable behavior pattern that has no apparent goal or function (Dantzer, 1986; Mason, 1991). The lack of function has traditionally been a differentiating characteristic, but it has been suggested that the behaviors may indeed have a short- or even long-term psychological effect on the performer (Mason, 1991). Whether this is a potential positive or negative effect remains unclear and may vary by individual.

The initial development of an abnormal behavior can be related to a variety of factors, including frustration, fear, or understimulation, such as displacement behaviors exhibited by animals unable to perform a desired natural behavior or those housed in a barren environment (Mason, 1991). Abnormal behaviors are also seen in conjunction with excitement or anticipation, suggesting they may provide the perception of control, a feature often limited in captive environments (Carlstead, 1996; Veasey, 2006). In any of these situations abnormal behaviors are examples of coping mechanisms, meaning they may help to decrease the physiologic effects of potential stressors (Carlstead et al, 1993; Mason & Latham, 2004). Individuals with a susceptibility to stress or those that lack natural coping abilities may be more prone to developing abnormal behaviors (Mason, 1991). Abnormal behaviors, especially stereotypies, are learnt over time, and their recurrent nature suggests that the animal is positively affected by the performance (Mason, 1991). Factors other than the initiating cause may alter the behavior's performance or appearance during its development and in time the original stimulus may no longer be required (Mason, 1991). Developed abnormal behaviors may therefore be performed in response to any potential stressor or even simply out of habit (Dantzer, 1986; Mason & Latham, 2004).

The distinctiveness in development and execution of abnormal behaviors makes comparisons between individuals difficult, as eliciting stimuli and physiological and behavioral responses vary both between and within species (Mason, 1991; Mason & Mendl, 1993). For instance, the performance of established abnormal behaviors can be influenced by such diverse variables as enclosure type, season, behavior of conspecifics, or scheduled events (Wilson et al, 2004), and hormonal research has linked the performance of abnormal behaviors with both high and low levels of stress hormones (Mason & Latham, 2004). Abnormal behaviors are seen in animals considered to have both good and poor welfare; individuals that differ in the presence or extent of these may be in similar welfare states, and a decrease in one individual's performance of an abnormal behavior does not necessarily indicate an increase in welfare (Carlstead, 1996; Mason & Latham, 2004; Mason & Mendl, 1993; Mason et al, 2007).

Abnormal behaviors are exhibited by an estimated 85 million captive animals worldwide, including those housed in laboratories, farms, houses, and zoos (Mason & Latham, 2004). Eliminating abnormal behaviors is difficult, and methods ranging from pharmaceuticals to positive reinforcement training have been utilized. Domestic and companion animals are often treated using punishment, which ignores the underlying motivation of the behavior and merely blocks performance (Mason et al, 2007). For zoos, the most common technique employed is enrichment. Enrichment is a husbandry practice aimed at increasing the physiological and psychological welfare of an animal through environmental augmentation (Swaisgood & Shepherdson, 2005). Enrichment is generally considered effective when it promotes more natural activity budgets but scientific evaluations of enrichment are uncommon (Swaisgood & Shepherdson, 2005). As opposed to pharmaceuticals or punishment, enrichment provides an animal with control and the ability to choose (Mason et al, 2007). Depending on the specific item, it may encourage natural behaviors, reduce the motivation to perform abnormal behaviors, or simply provide a time-consuming activity; however, novel enrichment is also potentially stressful and may exacerbate unwanted behaviors such as stereotypies or aggression (Carlstead et al, 1993; Mason et al, 2007). Therefore, enrichment ideally should be tailored to the individual animal (Mason et al, 2007; Swaisgood & Shepherdson, 2005) and take into account factors such as natural behavior, age, sex, and sociality, and multiple types of enrichment will likely have to be implemented to determine which types are useful.

Most research into abnormal behaviors is focused on domestic and lab animals, but zoos offer an opportunity to examine and compare multiple environments and husbandry practices, and additionally house individuals with more diverse and complete histories (Mason et al, 2007). Carnivores and primates are the most extensively studied groups in zoos (Bashaw et al, 2001; Dantzer, 1986), but captive ungulates are known to commonly exhibit both oral and locomotory abnormal behaviors. Oral behaviors, such as non-food chewing, are thought a form of self-enrichment due to an inability to forage, whereas locomotory behaviors may be frustrated attempts to approach or escape a stimulus (Bashaw et al, 2001).

Elephants in zoos and circuses have been recorded swaying, nodding, trunk swinging, and pacing, among other abnormal behaviors (e.g. Elzanowski, 2006; Friend, 1999; Schmid, 1995). Unlike many other animals, elephants will often perform species-typical behaviors while displaying stereotypies, such as eating while swaying or dusting while head bobbing (Friend, 1999; pers. obs). Often these stereotypies are considered effects of lack of space or restriction of movement. Circus elephants, for instance, are typically kept in picket lines when not performing, which prevents any movement beyond one step forward or backward and restricts the performance of many natural behaviors (Friend, 1999; Friend & Parker, 1999; Schmid, 1995). Gruber et al (2000) found that picketed circus elephants performed abnormal behaviors an average of 46% of the time. Keeping circus elephants instead in pens has been shown to decrease the performance of stereotypies and increase natural behaviors (Friend & Parker, 1999; Gruber et al, 2000; Schmid, 1995), but other studies have shown an increase in stereotypic behavior when elephants were instead penned (Friend, 1999).

Individual elephants vary tremendously in the form, eliciting stimuli, and frequency of performance of these behaviors (Elzanowski, 2006) and more systematic research needs to be done to evaluate the occurrence in zoos.

Abnormal behaviors have not been documented as often in black rhinos as in African elephants, which could be because of a smaller captive population, less behavioral research, or lower occurrence. Those that are seen include locomotory stereotypies (swaying, pacing), oral stereotypies (chewing or licking non-food items), and excessive horn rubbing (Hutchins & Kreger, 2006). As with elephants, the form and frequency of performance of these behaviors varies by individual. However, not enough is known of wild rhino behavior to truly deem many of these as abnormal and little captive research has linked them with stress or boredom (Hutchins & Kreger, 2006). Increased behavioral studies both in the wild and in captivity may help to further elucidate the motivations behind these behaviors.

The Current Study

Despite being behaviorally very different, African elephants and black rhinoceroses present many of the same complications when housed in captivity. They are housed in small enclosures, frequently without foraging resources or natural substrates, kept in unnatural social groups, and display abnormal behaviors; physiologically, both species have population-wide health concerns and low reproductive success. These similarities prompted the current study, which compares the behavior and exhibit use of the African elephants and black rhinos housed at CMZ. The goals of this study were to determine how each species has adapted its natural behavior to its captive environment, and to show the individual differences evident within each species. Although conclusions relating to the captive population as a whole cannot be drawn based upon this small sample size, the results do present possible areas of further investigation at additional institutions (Saudargas & Drummer, 1996).

Chapter 1: The Behavior of Captive African Elephants and Black Rhinoceroses

Introduction

African elephants (*Loxodonta africana*) and black rhinoceroses (*Diceros bicornis*) are considered flagship species in American zoos: both are recognizable mammals that help draw visitors into zoological institutions. The two species have many physiological similarities because of evolving in the same habitat and utilizing the same food resources, including large bodies, a prehensile appendage for browsing, and armaments possessed by both males and females (Archie et al, 2006; Estes, 1991). Despite this, African elephants and black rhinos are behaviorally very different. Elephants are active, moving and foraging for up to 20 hours per day; they are highly social and live in matriarchal groups consisting of related females and offspring (Estes, 1991; Vidya & Sukumar, 2005). Rhinos can spend up to half the day sleeping and wallowing, and as adults are solitary (Hutchins & Kreger, 2006; Schenkel and Schenkel-Hulliger, 1969). These similarities and differences are fundamental variables in determining how best to manage each of these species in captivity.

In captivity both elephants and rhinos are faced with similar challenges. Captive enclosures cannot replicate the size and environmental diversity of the African savannah (Mench & Kreger, 1996; Veasey, 2006), resulting in decreased space and sensory stimulation. Natural diets of browse are replaced with hay and concentrated pellets, reducing the need and ability to forage (Hutchins & Kreger, 2006; Stoinski et al, 2000; Wiedenmayer, 1998). Animals are often housed in unnatural social groupings: elephants are generally kept in small unrelated groups that may never interact with calves, males, or other groups of females (Hutchins, 2006; Olson & Wiese, 2000; Schulte, 2000); rhinos may be housed with other adult rhinos, both male and female (Hutchins & Kreger, 2006). These changes in the natural physical and social environments may be associated with the health and behavioral problems seen in both species, such as obesity, low reproduction rates, calf mortality, stress, and stereotypy (Carlstead et al, 1999b; Hutchins, 2006; Price & Stoinski, 2007; Veasey, 2006).

An additional management parameter that has sparked debate within the zoo community is climate, specifically whether northern U.S. zoos can successfully maintain these African species. The colder winter and unpredictable autumn and spring seasons in the northern U.S. often result in elephants and rhinos being housed indoors for longer periods of time. Indoor enclosures are often smaller and less environmentally diverse than outdoor enclosures, leading to speculation that increased indoor housing results in boredom, lethargy, or abnormal behaviors (Hutchins, 2006; Veasey, 2006). However, no research is available documenting seasonal behavioral patterns in elephants and rhinos housed at northern zoos.

All species have the ability to adapt their behavior to changes in environmental or social surroundings, and the degree to which an animal adapts to the conditions of captivity depends upon its species natural behavior and its individual history and experiences (Carlstead, 1996; Freeman et al, 2004; Mason

& Mendl, 1993). Successfully housing an animal in captivity is dependent upon an understanding of both its natural behavior and the degree to which that behavior can be altered without affecting psychological or physical health (Veasey, 2006). The purpose of this study was to determine how two large-bodied African ungulate species adapted their natural behavior to a captive environment, how the behavioral patterns of each species were affected by the seasonal changes of a northern climate, and how the behavior of African elephants and black rhinos may relate to husbandry practices and overall well-being. Based upon each species' natural history, elephants were expected to be more active than rhinos and both species were expected to decrease activity at higher temperatures. Activity levels were also predicted to decrease when animals were housed in indoor enclosures versus outdoor enclosures due to less available space and fewer behavioral options. Lastly, social relationships within each species were examined, and groups were expected to have stable relationships with little aggressive behavior.

Methods and Materials

Subjects

Subjects included three unrelated female African savannah elephants (*Loxodonta africana*), and one male and two related female eastern black rhinoceroses (*D.b.* michaeli) housed at Cleveland Metroparks Zoo (Table 1). All subjects could be easily visually identified.

Table 1: African Elephants and Black Rhinoceroses at Cleveland Metroparks Zoo

	Name	Sex	Yr. Born	Birth	Captivity	To CMZ
Elephant:	Jo	F	1967	Wild	1969	1997
	Moshi	F	1976	Wild	1978	1997
	Tika	F	1985	Wild	1983	1997
Rhino:	Jimma	M	1990	Captivity	n/a	2005
	Inge	F	1993	Wild	1997	1997
	Kibibbi	F	2003	Captivity	n/a	2003

Both species were handled under a protected contact system which included daily training sessions and daily or semi-daily presentation of enrichment (Table 2). Hay and fresh water were available to the animals throughout the day.

Table 2: Types and Examples of Enrichment Items Presented to Subjects

	Elephant	**Rhino**
Natural	Log, shavings	Branch/log
Artificial	Scrub brush, ball	Scrub brush, ball, bucket
Food	Browse, produce	Browse, hay cubes, produce

Housing

Subjects were housed in exhibits consisting of indoor and outdoor enclosures. Subjects were primarily observed in the indoor enclosures only during inclement weather and/or low temperatures. When the animals were housed inside and ambient temperatures allowed, the doors of the enclosures remained open to allow for air circulation. When temperatures dropped below approximately 10°C the enclosure doors were closed and the buildings were maintained at 18-21°C.

Elephant: The elephants were housed in the CMZ Pachyderm Building and adjacent outdoor enclosure (see Appendix 1). The indoor enclosure consisted of two stalls (each 77.77 m^2) and a bathing/holding area (18.83 m^2) with concrete substrates. When housed inside, two elephants were held in one stall and one elephant in the remaining stall; the shift door between the two stalls was kept slightly ajar to permit some interaction between all individuals. The ceiling contained multiple skylights and artificial lighting was only used when needed by the keepers. Zoo visitors could enter the Pachyderm Building to view the elephants but remained at a minimum distance of approximately two m. The outdoor enclosure was approximately 1416 m^2 with level ground composed of various substrates, and included a pool, mud wallow, rock for scratching, and multiple trees protected with fencing. The enclosure perimeter not adjacent to the Pachyderm Building (69.52% of the total perimeter) was surrounded by a moat, followed by a landscaped grass area and fence. The public had access to the entire fence line, at a distance of approximately three m from the elephants.

Rhino: The rhinos were housed in an indoor barn with two adjacent outdoor yards (see Appendix 1). The indoor enclosure contained five adjacent stalls (each 29.77 m^2) with concrete substrates. When housed inside the rhinos were given access to more than one stall but the male was separated from the females. The stall walls consisted of four horizontal metal bars that allowed for visual, oftactory, auditory, and some tactile contact between separated individuals. The ceiling contained multiple skylights and artificial lighting was only used when needed by the keepers. Zoo visitors could not enter the rhino barn but instead utilized a large viewing window at the front of the barn above the animals' level. The front outdoor enclosure was approximately 2160 m^2 and consisted of both level and sloped areas composed of various substrates, and included a pool, mud wallow, and multiple logs and wooden scratching posts. Two viewing platforms were available for zoo visitors, both directly above the animals' level; these platforms accounted for approximately 17.22% of the exhibit perimeter. The remaining perimeter consisted of either tall vertical wooden plank fencing, rock walls, or short post fencing with a top rail and bottom wire backed by thick shrubs. The back outdoor enclosure was approximately 500 m^2 and was separated from the front enclosure with a vertical plank fence. Rhinos had auditory and olfactory contact between enclosures but not visual or tactile contact. The rear wall was composed of vertical plank fencing and was directly adjacent to a service road used by zoo employees, visitors, and maintenance vehicles. The female rhinos were only observed in the front yard; the male rhino was observed in both the front and back yards.

Data Collection and Analysis

Animals were observed from the public viewing areas of their exhibits. Data on behavior and social proximity were collected using 20-minute continuous focal animal observations, allowing for frequency, rate, and bout lengths to be accurately calculated (Crockett, 1996; Lehner, 1996). Ethograms were exhaustive and mutually exclusive (see Appendix 2). Data were recorded on the HP® iPAQ pocket PC h2215 using Pocket Observer® 2.0 software (Noldus Information Technology, Inc, Wageningen, The Netherlands). Each subject was observed once per day, three days per week between 0900 and 1700 hours. Observations were balanced between AM (900-1259) and PM (1300-1700) hours. The order in which individuals were observed was randomized to eliminate observer bias (Altmann, 1974). Independent variables noted before each observation included enrichment presence [yes, no], ambient temperature [degrees C], and weather conditions [sun, clouds, overcast, rain, snow]. Data were collected on the elephants from September 2005 through January 2007 for a total of 201 hours; data were collected on the rhinos from June 2006 through July 2007 for a total of 156 hours.

Data were summarized using Noldus Observer® 5.0 (Noldus Information Technology, Inc, Wageningen, The Netherlands) and Microsoft® Excel XP software (Microsoft Corporation, Redmond, WA). Because of the small sample sizes results are presented using descriptive statistics; differences between condition means were considered significant if there was no overlap in SEM (Crockett, 1996; Kuhar, 2006). Activity budgets were calculated by averaging the monthly time (min/hr) individuals spent exhibiting each behavior and averaging those values within each species. Rhino data were also summarized to compare adults vs. juvenile and male vs. females. Only observations in which subjects were housed socially were included in analysis of social behavior. Seasonal changes were calculated by averaging species values for months within each season (Table 3); all other results include data from all months. Results are presented as average time displaying behavior (min/hr); bout lengths are presented as average time (s). All results are mean±SEM unless otherwise noted. The following variables were compared between species: enclosure (inside vs. outside); time of day; ambient temperature; weather; season.

Table 3: Months Averaged to Calculate Seasonal Totals

Spring	March, April, May
Summer	June, July, August
Fall	September, October, November
Winter	December, January, February

Results

To compare overall activity, behaviors were divided into Inactive (Sleep, Rest Alert, Lie Down) and Active (all other behaviors). The elephants were more active than the rhinos, averaging 52.92±1.01 minutes of activity per hour. The rhinos had similar values for activity (29.01±5.14) and inactivity (29.59±4.89). Time spent not visible averaged 0.19±0.22 min/hr with no significant difference between species.

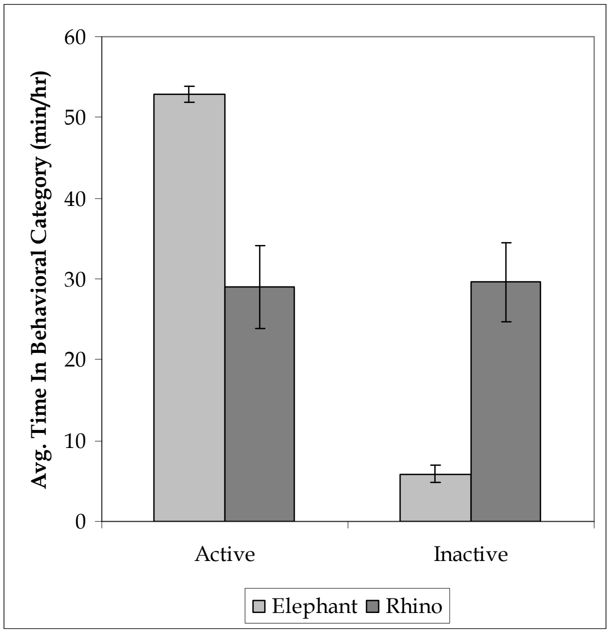


Figure 1. Mean levels of activity and inactivity in African elephants and black rhinos. The elephants averaged more time per hour performing active behaviors. The rhinos had similar levels of activity and inactivity.

Species differed in performance of specific active behaviors. The rhinos spent less time eating and more time locomoting, and also had longer bouts of locomotion than elephants (24.08±4.96 vs. 11.84±0.82 s). Elephants spent a larger amount of time displaying environment-oriented behaviors (including Rub, Wallow, Dust, Dig, and Investigation [object and enrichment]).

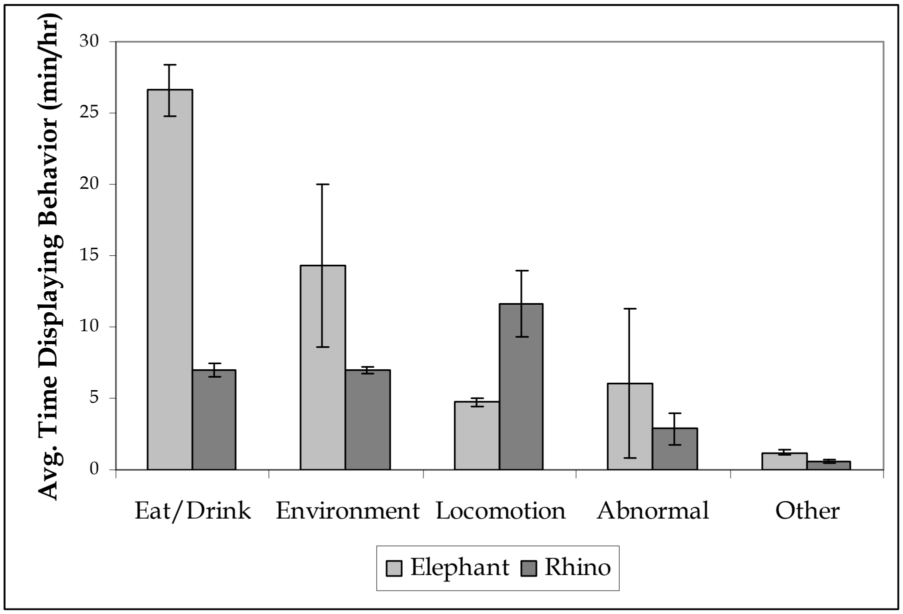


Figure 2. Mean time performing active behaviors. The most common active behaviors in the elephants were eating and environmental investigation, both of which were at significantly higher levels than in the rhinos. The rhinos locomoted more than the elephants. There was no significant difference in performance of abnormal behaviors.

Hourly Trends

Few behaviors varied throughout the day. In both species time spent eating rose slightly at 1000 and 1300 hrs, which would correspond to approximate feeding times.

Rhinos had a peak in resting at 1300 hrs, with near-mirrored values both before and after. Elephants showed virtually no change in their Resting behavior until late afternoon, and the following rise was comparatively small. No other significant changes were observed.

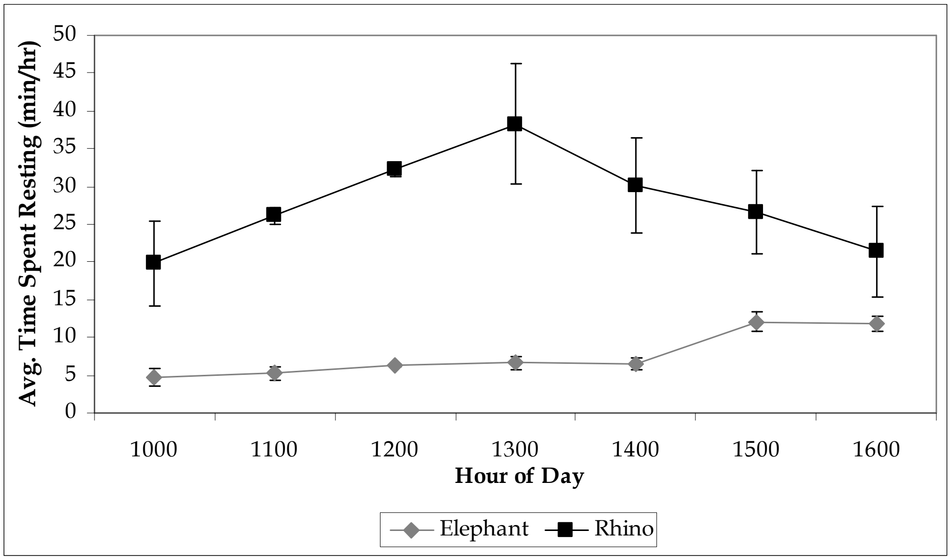


Figure 3. Mean resting behavior in relation to time of day. Elephants showed little change in resting until late afternoon, whereas rhinos had a peak in resting behavior at midday and more variability in the afternoon.

Seasonal Trends

Seasonal changes in behavior also show differences between species. In elephants, average time spent locomoting fluctuated less than four minutes throughout the six seasons they were observed. In rhinos this behavior was variable, with higher in the fall and lower levels in the winter and spring.

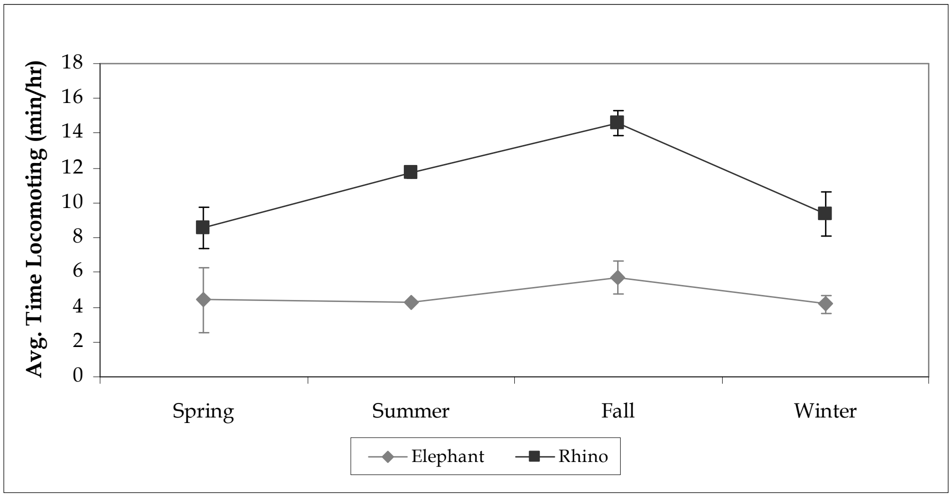


Figure 4. Seasonal trends in mean locomotion. Elephants showed little change across seasons. Rhinos had higher levels during summer and fall months, suggesting that increased time spent outside may encourage more locomotion.

Rhinos showed no other seasonal trends in behavior. In the elephants, investigation (object and enrichment) was lowest during the winter and most variable during the winter and spring. Environment-oriented behaviors (rub, dig, dust, wallow) were highest in the spring and summer and lower in fall and winter.

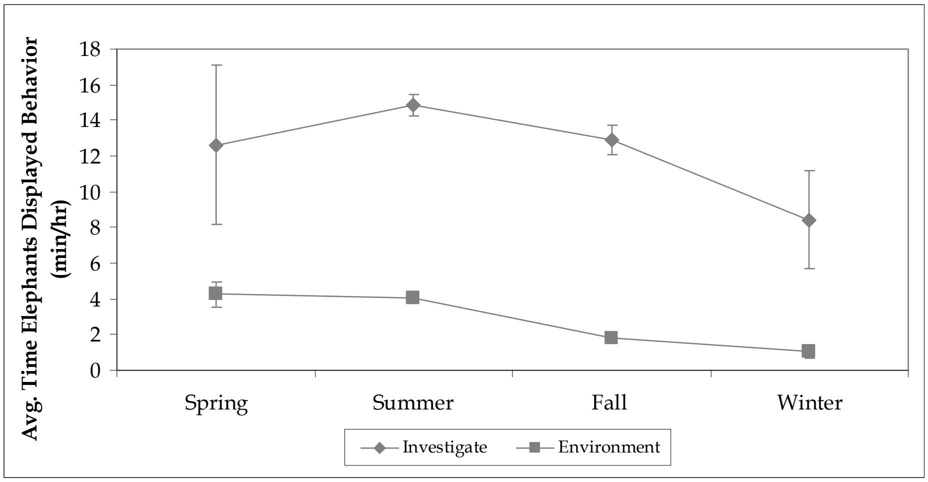


Figure 5. Seasonal changes in mean investigatory and environmentally-oriented behaviors in African elephants. Subjects decreased performance during winter months, suggesting increased time inside may discourage performance of these behaviors.

Temperature and Weather Trends

The only behavior correlated to ambient temperature in elephants was Dusting. Elephants increased dusting with increasing ambient temperatures, averaging more than 10 minutes/hour dusting at temperatures above 30°C.

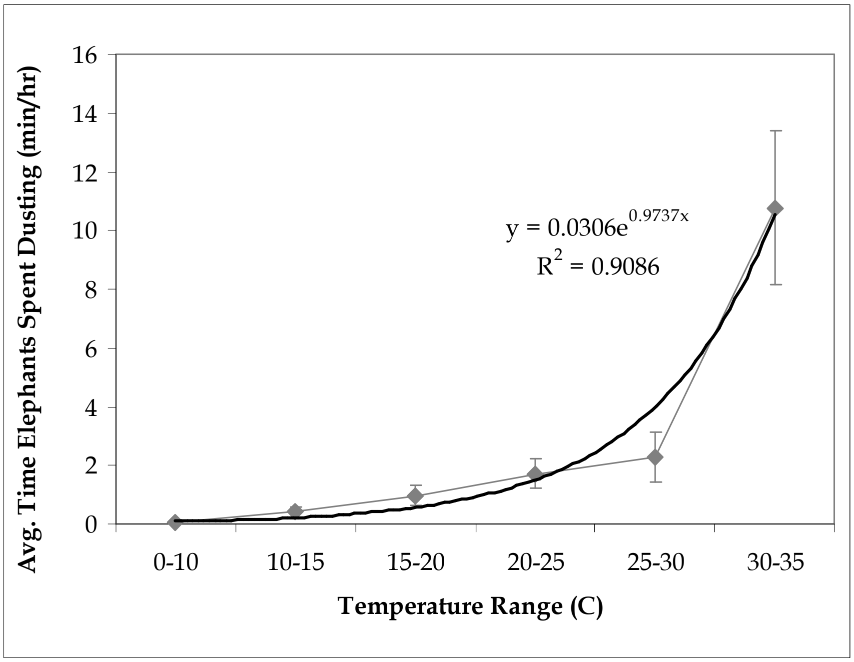


Figure 6. Temperature-related trends in dusting behavior in African elephants. Data include only time subjects were housed in the outdoor enclosure. Elephants increased time spent dusting with increasing ambient temperatures, resulting in a logarithmic relationship.

Rhinos increased resting behavior with increasing temperatures, which was not seen in the elephants.

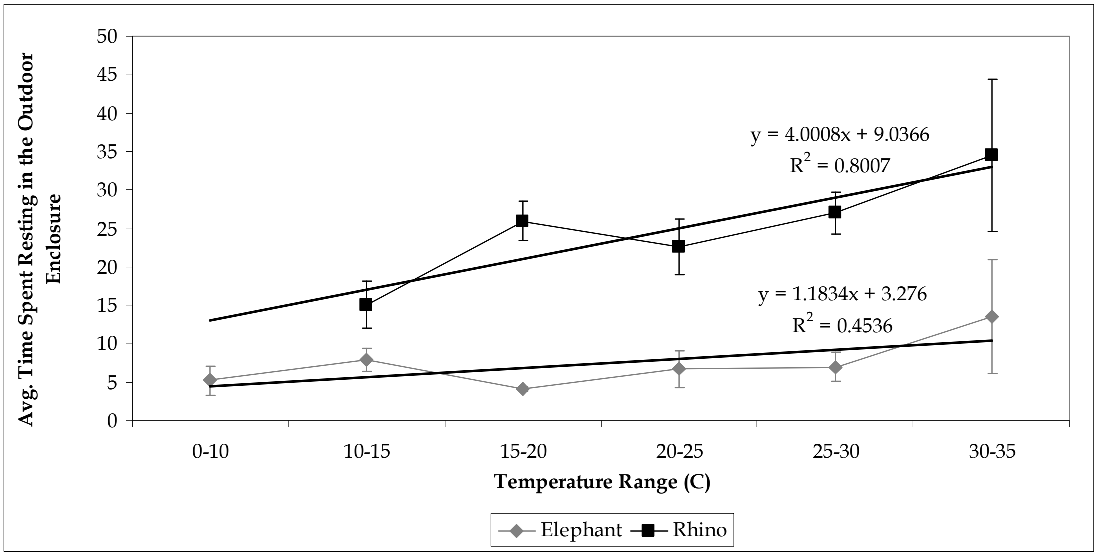


Figure 7. Temperature-related trends in average resting behavior. Data include only time subjects were housed in the outdoor enclosure. Elephants had no significant difference across temperatures. Rhinos showed a trend of increased resting behavior with increasing ambient temperature.

Weather condition independent of temperature was also analyzed. There were no significant changes but each species showed trends in activity: with increasing amounts of sun the elephants decreased object investigation and the rhinos increased rest, bathe/wallow, and dig.

Social Proximity and Behavior

Proximity data include only outside observations to ensure no forced proximity, and do not include the male rhino as that subject was always housed solitarily.

Both species were distant from conspecifics more often than proximate and average bout lengths of remaining distant were similar. Elephants were in social proximity more often than rhinos and averaged longer proximity bout lengths. Proximity did not change with time of day, temperature, weather, or season.

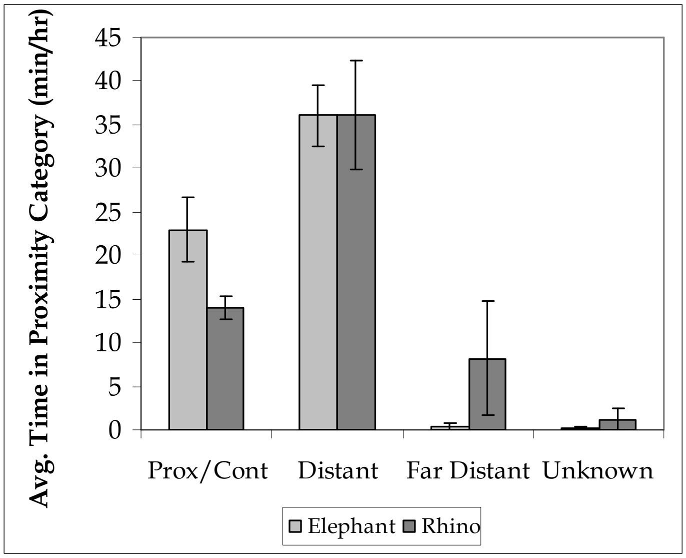


Figure 8. Mean time spent in social proximity. Elephants and rhinos spent most time distant from conspecifics. Elephants were in proximity or contact significantly more than rhinos, and rhinos were out of sight of conspecifics more than elephants.

Elephants did not differ significantly in total social behavior between enclosures (inside: 0.87±0.19, outside: 0.64±0.12 min/hr). The female rhinos had a larger variation, with significantly more total social behavior inside (1.59±0.25 min/hr) than outside (0.37±0.02 min/hr). The rhinos displayed very few agonistic and other social behaviors outside.

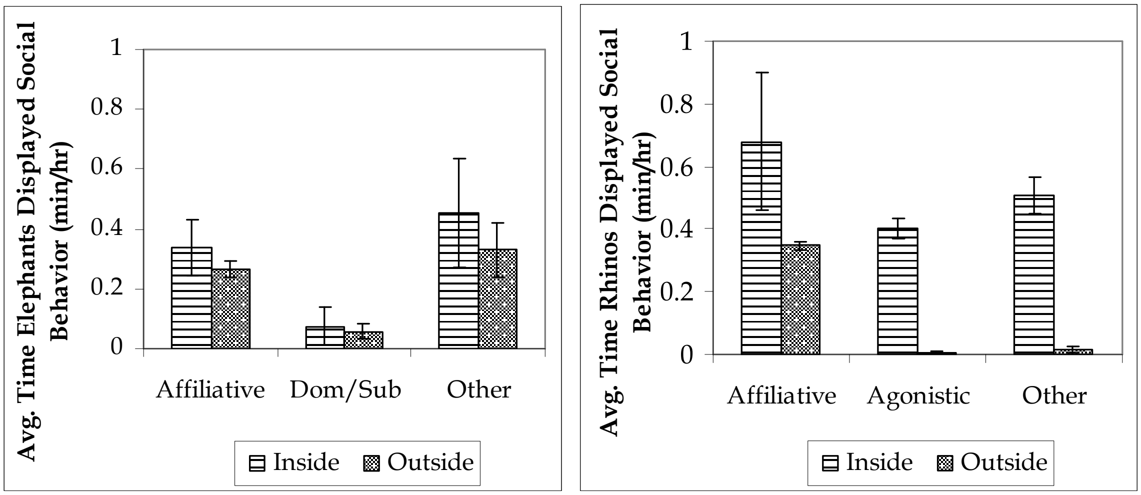


Figure 9. Mean occurrence of social interactions in each enclosure in the elephants (A) and rhinos (B). Elephants did not differ significantly in social behavior between enclosures. Rhinos displayed significantly more social behavior inside, and showed little agonistic and other behaviors outside.

In the elephants total social behavior was greater during PM hours (0.94±0.04 vs. 0.43±0.01 min/hr AM), with large increases in affiliative and other interactions. The rhinos also had higher levels of social behavior during PM hours (1.87±0.30 vs. 0.98±0.39 min/hr AM), with the largest increase in other behavior. No trends in social behavior in either species were evident in relation to season, temperature, or weather.

Discussion

Overall Activity: As expected, the elephants were more active than the rhinos; the former rested for less than five min/hr, while the latter did so for approximately 30 min/hr. In the wild elephants rest for only four to six hours each day, the majority of their time being spent feeding and foraging (Estes, 1991; Spinage, 1994; Wyatt & Eltringham, 1974). The data from this study would correspond to only two hours per day, but longer bouts of sleeping typically happened in the early morning hours before data collection began and are therefore not reflected in the results. Rhinos in the wild spend up to half of their day sleeping and wallowing (Kiwia, 1986); although this study did not group wallowing into the resting behaviors, it accounted for less than 1.5 min/hr of activity in each individual and was only seen outside. The rhinos rested most in the early afternoon, while the elephants did not show significant differences in the behavior throughout the day. These different trends correspond to differences in natural behavior: elephants rest for short periods of time throughout the day as they move and forage, whereas rhinos are inactive for long stretches during the late morning and early afternoon when temperatures are highest (Estes, 1991; Hutchins & Kreger, 2006; Kiwia, 1986; Schenkel & Schenkel-Hulliger, 1969; Spinage, 1994). Resting behavior and patterns in both species were therefore similar to expected values based upon natural activity budgets.

The elephants locomoted for an average of 4.72±0.31 min/hr, or approximately 8% of the total activity budget. These results are similar to the average daytime locomotion rate of captive female elephants seen by Stoinski et al (2000). Comparisons of captive locomotion levels to wild populations of elephants and rhinos are difficult. Elephant herds typically walk while foraging, moving at a consistent and slow pace of about 0.5 km/hr with the overall amount of locomotion depending upon multiple factors such as habitat quality, population size, and season (Estes, 1991; Spinage, 1994; Wyatt & Eltringham, 1974). When browse is plentiful herds may walk only 10-15 km in a day, and during the dry season when food is scarcer herds have been reported to travel as much as 80 km in a day (Hutchins, 2006; Spinage, 1994). Rhinos also vary their movement patterns, walking primarily to find food, water, and sites for wallowing or resting (Schenkel & Schenkel-Hulliger, 1969). The rhinos locomoted significantly more than the elephants, averaging 11.59±2.33 min/hr, or approximately 19.32% of their total activity budget. Kiwia (1986) documented wild black rhinos as walking 14.2% of their total activity budget during the wet season and 22.1% during the dry season, rates similar to those found in this study.

Resource availability is clearly a factor in the daily activity patterns both species in the wild, and other influences include season, geographical location, and even activities of other herds and individuals (Estes, 1991; Hutchins, 2006; Hutchins & Kreger, 2006; Schenkel & Schenkel-Hulliger, 1969). In captivity, however, resources are presented to the animals and condensed within a small area, and environmental and social variables are relatively static. Eliminating the primary reasons for elephants and rhinos to move may decrease the psychological need for increased movement and is likely to result in smaller locomotion rates than what is seen in the wild. Adequate exercise is necessary to maintain physical and psychological health and provided these needs are met it may not be necessary for animals to locomote more. Determining appropriate amounts of exercise should therefore not be based solely upon movement levels of wild animals but rather a combination of natural behavior and measures of individual health, such as overall behavioral repertoires, body condition, arthritis, and age. Future work at multiple institutions that incorporates both behavioral and physiological data is necessary to assess proper movement levels of these species.

Feeding: Feeding was the most common behavior observed in the elephants, averaging 26.61±1.79 min/hr (approx. 44%). Little data are available regarding time elephants spend feeding in captivity. Separate studies of one captive group found feeding rates between 20% and 50% of total activity depending on time of day (Brockett et al, 1999; Stoinski et al, 2000; Wilson et al, 2006); reported feeding rates of wild elephants range from 74.2% to 90% (Estes, 1991; Spinage, 1994; Wyatt & Eltringham, 1974). The rhinos spent considerably less time feeding, averaging only 6.98±0.47 in/hr (approx. 12%). Few wild or captive studies have examined rhino feeding behavior, but Kiwia (1986) found average feeding rates of black rhinos in Tanzania ranging from 15.8% in the dry season to 31.7% in the rainy season. Feeding times of both the elephants and rhinos were less than average rates in the wild. This decrease is likely due to the different food sources of wild elephants and rhinos: both species are browsers, and the leaves, sticks, and bark they feed upon in the wild take longer to manipulate and eat than does the hay and grain commonly fed in captivity. A captive study by Stoinski et al (2000) found that an equal amount of browse instead of hay increased feeding time in African elephants from 50% to 80%, and additionally increased overall activity and public visibility. Feeding and foraging are basic behavioral needs and animals are often highly psychologically stimulated to perform the behaviors even if not nutritionally required to do so (Veasey, 2006). The time an animal spends feeding in captivity should therefore be similar to that of wild counterparts (Morimura & Ueno, 1999), and for African elephants and black rhinos this is dependent upon providing more natural food sources. Increasing the amount of browse in captivity can help to increase natural foraging and feeding behaviors and as a result may decrease the amount of time spent inactive or performing abnormal behaviors. Feeding a diet of exclusively browse is not practicable in captivity, but supplementing some of the traditional hay rations with equal amounts of browse encourages natural levels of feeding and foraging without increased amounts of food.

Heat Dissipation: African elephants and black rhinos are large mammals that inhabit warm environments, and each species has methods of dissipating body heat. In elephants this is done via dusting, or using the trunk to toss dirt and other substrates onto an individual's back and sides. Dusting was the only temperature-correlated behavior in elephants; the behavior increased with increasing temperatures but was seen in all temperature ranges. Although an elephant's skin is thick the blood vessels and nerves are relatively close to the skin and they have few sweat glands for heat dissipation (Adams & Berg, 1980; Rees, 2002). Dusting and mudding help to protect the skin from sun and insects, assist with temperature regulation, and encourage the shedding of dead skin cells (Rees, 2002). Adams & Berg (1980) reported that captive elephants performed the behavior more frequently when the temperature was greater than 27°C; Rees (2002) found the frequency of dusting in captive Asian elephants was linearly correlated with increasing temperatures, and as in this study there was no difference in individual rates based on age, mass, or reproductive condition. The temperature correlation found in this and other studies support the idea that the primary reason for dusting is reducing body heat, but dusting is also often performed after bathing, during social situations, and when anxious (Adams & Berg, 1980; Schmid, 1995). Elephants should therefore have the option of dusting not only when temperatures are high but at all times and in both outdoor and indoor enclosures.

Like elephants, rhinos have a large mass and only a small number of sweat glands (Benyus, 1992; Estes, 1991) and necessitate ulterior means of reducing body heat. They do not have the ability to throw substrates onto themselves and thus their method of dissipating body heat, gaining sun protection, and reducing insects is wallowing in mud (Hutchins & Kreger, 2006). Wallowing was not significantly correlated with temperature, but was seen more with increasing amounts of sunlight. Increased temperatures were associated with increased resting behavior, and resting was also highest during hotter hours of the day; this behavior is likely used in conjunction with wallowing to reduce body heat. These results suggest that rhinos adapt their overall activity budgets to temperature and weather conditions more so than elephants and rhino enclosures should provide enough mud wallows, resting sites, and shade structures for all individuals, and the conditions of mud wallows should be monitored at higher temperatures to assure rhinos have the option of wallowing.

Seasonality: Locomotion was the most commonly observed active behavior in rhinos, and investigatory/environmental behaviors were the most common active behavior in elephants next to eating. Rhinos locomoted least in the winter, which suggests that increased time in the indoor enclosure due to colder weather was associated with decreased locomotion. The highest level of locomotion in rhinos was in the fall, which may suggest that moderate temperatures encourage more activity than either cool or warm temperatures. Future studies comparing rhino behavior at zoos in warm, moderate, and cooler climates would be useful in determining the specific effect temperature has on locomotion and what climates are most conducive to encouraging natural levels of activity.

Seasonal trends in locomotion were not seen in the elephants, but object investigation and environment-directed behaviors were lowest in winter. Each species therefore showed a different behavior that was most affected by indoor housing. Housing animals in northern climates often requires increased time inside during colder months, typically in much smaller enclosures, and ideally this should not affect average activity budgets. Research at multiple institutions is needed to determine if these patterns are seen in other captive elephants and rhinos, including comparisons of northern and southern climates to clarify the effect of indoor housing. If rhinos in fact have a tendency to decrease locomotion when housed inside they may benefit from managerial changes designed to increase motivation to move, such as larger indoor exhibit areas, scattered food, or exercise programs implemented by keepers. Elephants may benefit from increased environmental complexity and variability to encourage investigatory behaviors, as well as substrates that allow digging, dusting, and manipulation. This does not minimize the need for appropriately designed rhino enclosures or adequately spacious elephant enclosures, but merely highlights how the two factors may not affect each species to the same degree.

Social Behavior: Maintaining functional social groups in captivity is a primary welfare concern (Frézard & LePape, 2003; Veasey, 2006). Most ungulate species can adapt to various social situations (Veasey, 2006), but if group structures differ from what is seen in the wild, as is often the case with African elephants and black rhinos, behavioral research can help determine whether these groups provide stable social environments. A primary indicator of social stability is lack of intragroup aggression (Hutchins, 2006; Veasey, 2006; Wilson et al, 2006), which was observed among both the elephants and rhinos. Overt aggression was never seen amongst the elephants at CMZ. Low rates of female aggression are common in both captive and wild groups of elephants (e.g. Archie et al, 2006; Adams & Berg, 1980; Brockett et al, 1999; Garaï, 1992; Gruber et al, 2000; Wilson et al, 2006; Wyatt & Eltringham, 1974). The elephants at CMZ interacted for less than one min/hr. Frézard & LePape (2003) reported a captive group of three female wolves that had been housed together for years and displayed little social behavior. Although not closely related to elephants, wolves have a similar social system: they generally live in related groups, have an intricate repertoire of social behaviors, and rely on conspecifics for survival (Mech, 1970); like elephants, wolves often must adapt to small, unrelated social groups in captivity. It is therefore possible that the small amount of social behavior seen in the CMZ elephants is due to familiarity and stability as suggested by Frézard & LePape (2003): the animals have established a dominance hierarchy and have no need to interact extensively.

Small amounts of social behavior were also characteristic of a group of three elephants housed at Zoo Atlanta (e.g. Brockett et al, 1999; Stoinski et al, 2000; Wilson et al, 2006); Wilson et al (2006) suggested it may also be due to age, as other species of ungulates decrease social interaction with age. It could also be a factor of the captive environment. Most of the factors that enhance social relationships among wild elephants are not present in captivity, such as entering a new environment, searching for food, or defending calves against predators, and thus individuals may decrease social behavior (Schulte, 2000). Each of these reasons suggests that captive elephant groups may have less immediate need to interact as compared to their social counterparts. This may also explain the elephants most often remaining socially distant in the outdoor enclosure, which has been reported in other captive groups (e.g. Brockett et al, 1999; Wilson et al, 2006). Lack of need to interact, however, does not negate the importance of conspecific companionship in this species. Social proximity and physical contact are vital components of elephant societies both in the wild and in captivity (Adams & Berg, 1980; Garaï, 1992). Even if social behavior is displayed for small amounts of time, captive elephants should always be housed in social groups to provide the opportunity for interaction.

Black rhinos are not a social species but inhabit territories shared by many conspecifics; thus they do not have the intricate social relationships of African elephants but still maintain methods of interacting with other rhinos. Kiwia (1986) found that black rhinos in Tanzania engaged in social behavior for only 1-2% of the total activity budget. The female rhinos at CMZ had similar levels, approximately 0.62% when outside and 2.65% when inside. Although the increase seen in the indoor enclosure may not be biologically significant due to the small values (Swaisgood et al, 2006), it is possible that it is the result of environmental and/or social factors. There was less available space and fewer behavioral options inside; the rhinos may have used social behaviors as a form of enrichment, or may have increased social interaction simply because of increased social proximity.

It is also possible that the increased social density of the indoor enclosure is stressful to this naturally solitary species, even when individuals are related. When housed outside the females most often remained distant from one another, but inside the rhinos had less control over their social proximity. Additionally, agonistic behaviors were seen significantly more often inside, which may suggest increased tension between the females. The aggression, however, was still relatively rare and never resulted in injury. Although black rhinos are naturally solitary, individuals can likely be housed together provided they have ample space to control social proximity and aggression rates are low. Evaluating social groupings of both black rhinos and African elephants in an effort to ensure compatibility may be beneficial for captive institutions. A better understanding of how these species interact with conspecifics in captivity will result in more informed decisions regarding social housing and management.

Summary and Conclusions

1. Average resting levels of African elephants and black rhinos were similar to expected values based on data from wild and captive studies.
2. Little comparative data is available to determine appropriate locomotion rates, but evaluating levels of exercise using physiological and health measurements in addition to natural behavior may be beneficial for animal managers.
3. Amount of time elephants and rhinos spend feeding may be increased through the use of more natural food items such as browse.
4. Both species adapted their behavior to high temperatures and increased sun exposure. Exhibits should include substrates for dusting, mud wallows, shade structures, and resting sites for all individuals.
5. Increased time spent inside during winter months was associated with decreased investigatory behaviors in elephants and decreased locomotion in rhinos. Indoor exhibits should include environmental variation, enrichment, and space so as to encourage these behaviors.
6. Social behavior in both species was a small portion of the activity budget. Little social behavior and low aggression rates suggest stable relationships, and stability and compatibility may be more important for proper social housing than strictly natural social groupings.

Chapter 2: Exhibit Use and Object Preferences of Captive African Elephants and Black Rhinoceroses

Introduction

The behavioral repertoires of both African elephants and black rhinos evolved in part based upon their natural environment, and thus providing appropriate enclosures in captivity is essential in promoting their well-being. Successful management and breeding of any animal in captivity requires assessment of how the animal utilizes its space, what aspects of the enclosure are effective in encouraging natural behaviors, and how possible sources of environmental stress can be minimized (Carlstead et al, 1993; Seidensticker & Doherty, 1996). Enclosure size and design can significantly affect activity budgets in captive animals, as inappropriate or barren environments can restrict the performance of natural behaviors and may result in abnormal behaviors (Lukas et al, 2003; Mallapur et al, 2002). Captive exhibits are generally more restrictive and less dynamic than wild habitats, often resulting in enclosures that are too small or unable to meet an animal's physical and behavioral needs (Frézard & LePape, 2003; Mench & Kreger, 1996). Captivity also imposes upon animals numerous environmental aspects not present in the wild, requiring individuals to adapt their behavior to cope with these possible stressors. Zoos require animals to remain in a static environment with space limitations, feeding schedules, forced social grouping, and restriction of natural resources such as browse (Lukas et al, 2003; Seidensticker & Doherty, 1996). Evaluating how animals utilize their captive environments is a vital component in determining proper standards in husbandry and housing, but little information is available detailing this variable in African elephants and black rhinos.

The natural history of a species in relation to its habitat is important in determining appropriate exhibit specifications (Morgan & Tromborg, 2007). Female elephant herds base their movement upon food availability; during the rainy season when food is plentiful ranges are smaller, whereas a lack of food and water resources during the dry season results in elephants having to range further to meet their physical needs (Hutchins, 2006; Spinage, 1994). Home ranges as varied as 14 to over 3500 km^2 have been reported in Africa (Spinage, 1994). Black rhinos also vary their activity depending upon resource distribution, specifically food, water, and wallowing sites; reported home ranges in this species are from three to over 500 km^2 (Hutchins & Kreger, 2006). Environmental resources are therefore the primary motivator of activity of both species, and each can adapt to various wild habitats provided ample resources are available (Estes, 1991).

The ability to alter behavior in order to cope with various habitats in the wild suggests that African elephants and black rhinos can successfully adapt to captive environments if given appropriate space and resources. The purpose of this study was to determine how the behavior of the elephants and rhinos housed at CMZ differed between the indoor and outdoor enclosures and how the subjects utilized the space and objects within each enclosure. Subjects were expected to show more environment-oriented species-typical behaviors (including investigation, rubbing, and scent marking) when outside because of the more naturalistic enclosure spaces, and when housed outside subjects were expected to use all areas of the enclosure equally. As the indoor enclosures were small and less complex, subjects were predicted to increase the performance of abnormal behaviors as well as increase the use of enrichment items when housed inside. The results suggest how enclosures can best be designed to encourage natural behaviors and how husbandry practices such as enrichment can potentially supplement overall environmental composition.

Methods and Materials

Subjects and Housing: Please refer to Chapter 1 Methods and Materials for information on subjects, management, and housing.

Data Collection and Analysis: Please refer to Chapter 1 Methods and Materials for data collection and analysis protocols.

Behavior results are presented as average time displaying behavior (min/hr); bout lengths (time of one behavioral stint) are presented as average time (s); preferred objects for rub and investigate are presented as percentages of total time spent exhibiting that behavior based on species activity budgets; average number of urine sprays is presented as number of occurrences per hour.

Outdoor exhibits were visually divided into multiple sections based on primary environmental features; exhibit use was determined by time spent in specific enclosure area. The percent of time spent within each enclosure area was compared with that area's approximate physical percentage of the exhibit to determine observed versus expected exhibit use values. All results are mean±SEM unless otherwise noted. The following variables were compared between species: enclosure (inside vs. outside); enrichment presence; time of day; ambient temperature; weather.

Results

Indoor vs. Outdoor Enclosure: Both elephants and rhinos increased object investigation in the outdoor enclosures. Elephants additionally increased enrichment use and decreased abnormal behavior outside; rhinos rested less outside.

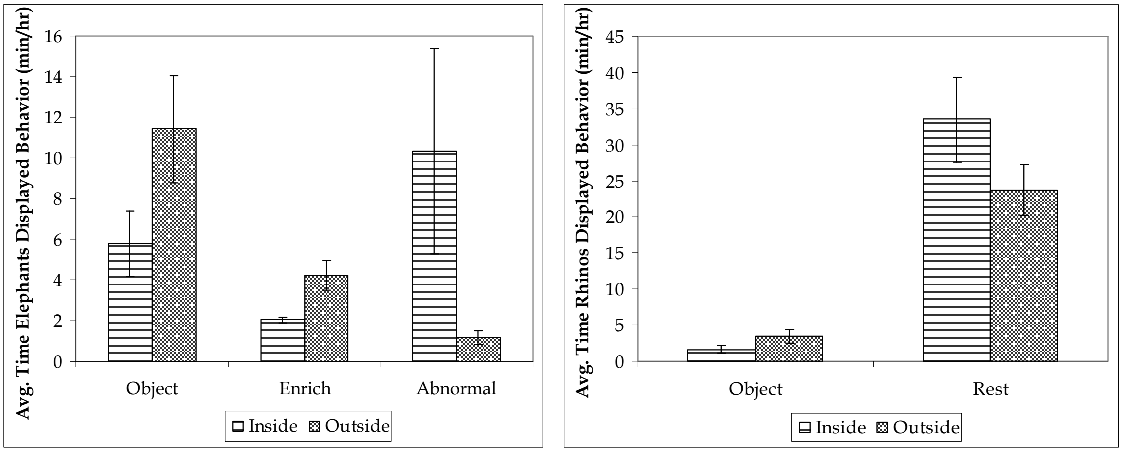


Figure 1. Changes in behavior in the indoor versus outdoor enclosure in elephants (A) and rhinos (B). Elephants increased investigation of both environmental objects and enrichment and significantly decreased abnormal behaviors. Rhinos slightly increased object investigation and decreased resting.

Abnormal behavior was not affected by temperature when the elephants were housed inside, but when outside the behavior was greater when the temperature was below 10°C (3.90±1.97 min/hr) than in higher temperature ranges (avg. 0.68±0.23 min/hr).

The male rhino urine sprayed an average of 5.06±0.76 times each hour when inside and 7.97±1.84 times each hour when outside. The females displayed the behavior far less frequently, averaging 0.80±0.09 urine sprays per hour with no difference between enclosures.

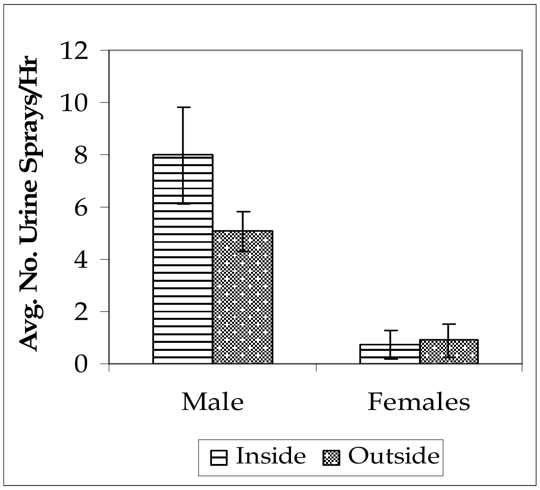


Figure 2. Occurrence of urine spraying in the male and female rhinos. The male rhino had overall higher mean rates of urine spraying and performed the behavior more in the indoor enclosure. The females showed no difference based upon enclosure.

Both species rubbed more in the inside enclosure, and in both enclosures rhinos rubbed more than elephants (Avg. min/hr: Elephant 0.34±0.1 in, 0.17±0.06 out; Rhino 2.12±0.36 in, 1.49±0.75 out). When inside both species most frequently rubbed against the walls, doorframes, and bars of the enclosure (mean prob.

0.81±0.07), but outside the objects chosen were more variable: elephants most often rubbed against the exterior of the holding facility, while rhinos frequented the trees and logs within the exhibit.

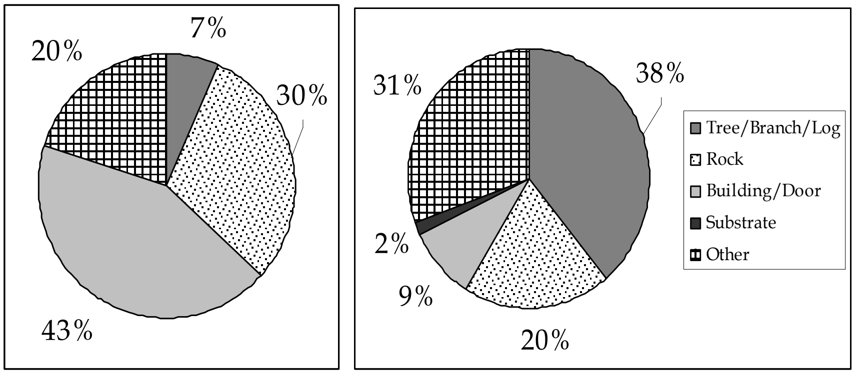


Figure 3. Object preferences for rubbing in elephants (A) and rhinos (B). Data include only time spent in outdoor enclosures. Both species utilized multiple exhibit objects. The elephants most often rubbed on the building; the rhinos most often rubbed on trees or logs.

Enrichment: When presented with enrichment items in the inside enclosure both elephants and rhinos averaged between two and three minutes of investigation per hour. Outside this nearly doubled to over 4.5 min/hr in elephants. Rhinos decreased enrichment use slightly when outside, but the difference was not significant. Although the adult rhinos did not differ in average enrichment investigation, the juvenile used enrichment items significantly more than adults both inside and outside.

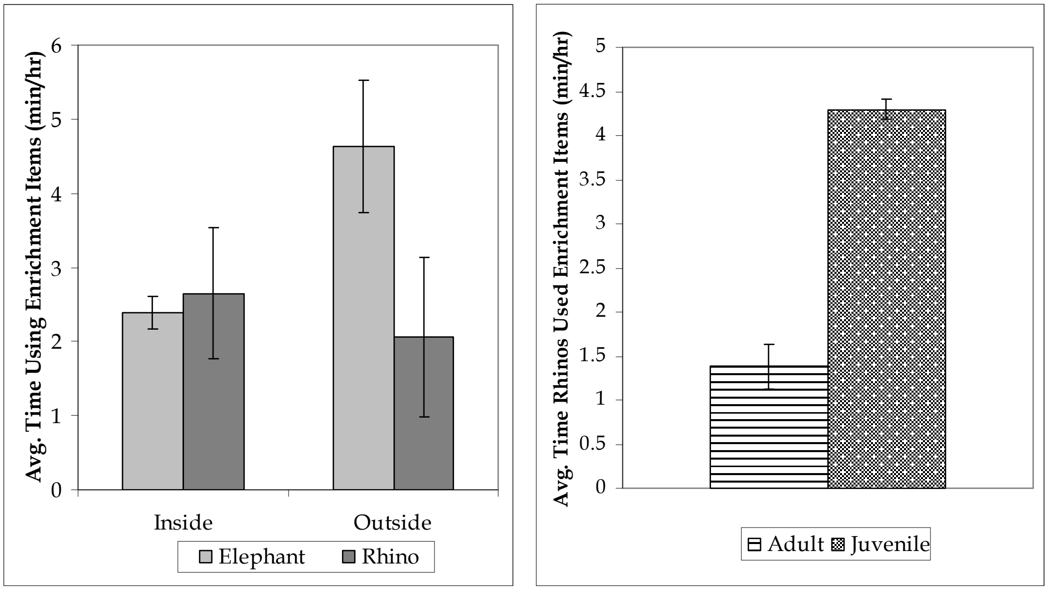


Figure 4. Mean enrichment use by species (A) and based upon age in rhinos (B). Data on adult and juvenile rhinos based upon both indoor and outdoor observations. Species had similar levels of enrichment use when inside; elephants increased enrichment use when outside. Among the rhinos, the juvenile used enrichment items more often than the adults.

Three types of enrichment items were provided: Natural, Artificial, and Food (see Chapter 1, Table 2). Natural and Food enrichment elicited the longest investigatory bouts in both species; elephants averaged longer usage bouts than rhinos in both cases. Bouts of Artificial enrichment investigation averaged less than 30 sec. in both species.

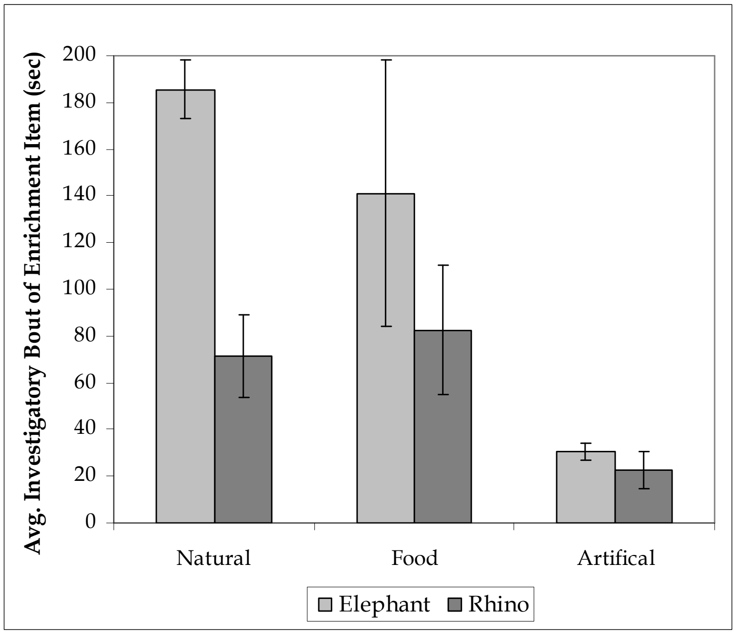


Figure 5. Mean investigatory bouts of different categories of enrichment. Both species used natural and food enrichment items for longer periods of time than artificial items. Elephants tended to have longer overall bouts, though the difference was only significant with natural enrichment.

Elephants showed no changes in investigatory bout length between enclosures, but rhinos averaged longer bouts of Artificial enrichment investigation inside (30.44±2.87 s) than outside (14.85±4.15 s).

The presence of enrichment in the outdoor enclosure correlated with a decrease in mean resting (3.34±0.99 versus 8.39±1.83 min/hr) and dusting (1.12±0.28 versus 1.8±0.18 min/hr) behavior and increase in social behavior (0.38±0.13 versus 0.77±0.15 min/hr) in the elephants. Enrichment presence was also associated with increased time spent near the Building and decreased time near the Trees. Enrichment presence was not associated with any behavioral changes in the indoor enclosure. Rhinos were observed with various enrichment items within their enclosures on a daily basis and thus behavior could not be analyzed to compare changes between enriched and non-enriched days.

Outside Exhibit Use: Elephants and rhinos differed in time spent within each enclosure area. Both species spent more time than expected near the Building and Door and less time than expected near the Water Source and Public Viewing Area; the two species differed in use of the Trees and Wallow. The female rhinos spent less time and the male more time than expected in the Rear Perimeter.

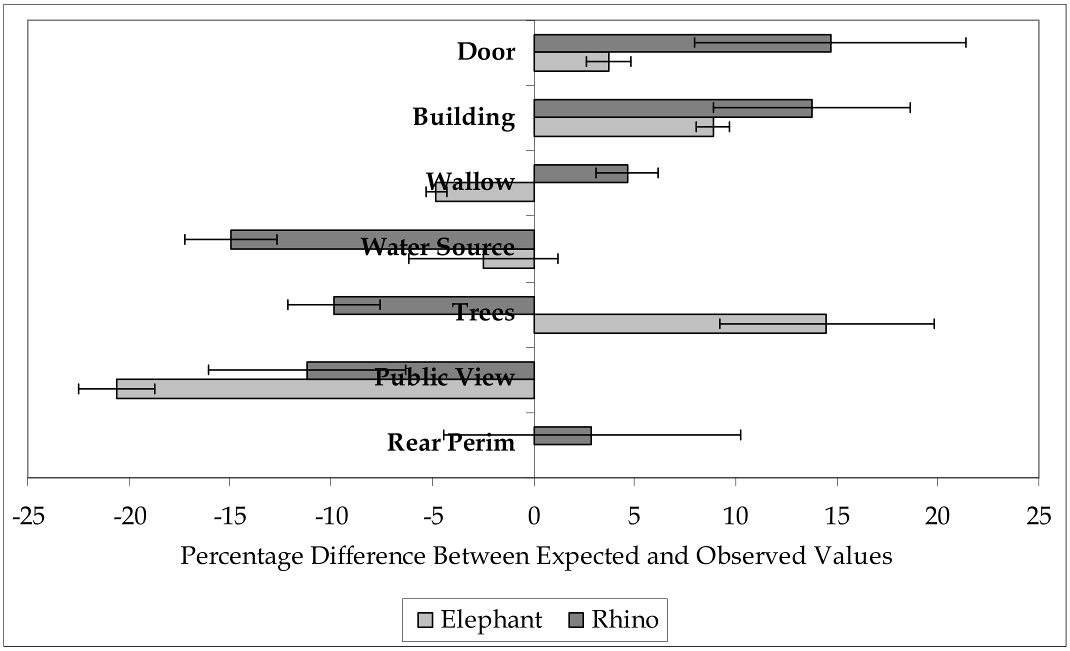


Figure 6. Actual versus expected use of exhibit areas. Expected use based upon size of given area as a percentage of entire exhibit. Both species were in the Door and Building areas more than expected, and spent less time than expected in the Public View areas. Elephants used the Tree area and rhinos the Wallow more than expected.

The average bout of time spent in each area varied between species. Elephants overall remained in one area for a longer time period than rhinos, though species showed similar bouts near the Mud Wallow and Public Viewing areas. Elephants had longer bouts near the Trees and Water Source than in other areas, while rhinos had longer bouts near the Trees, Public Viewing, and Rear Perimeter areas.

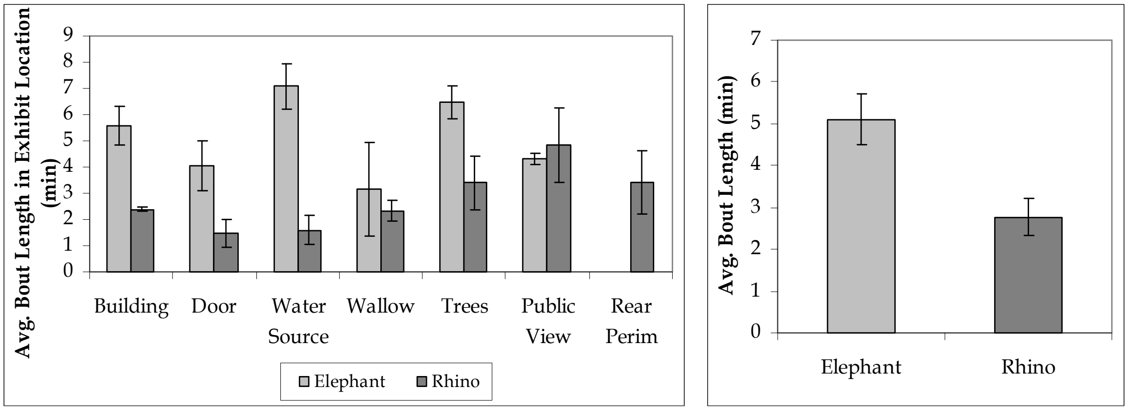


Figure 7. Mean bouts spent in each exhibit area (A) and by each species (B). Species means include data from all exhibit areas. Elephants and rhinos had similar bouts in the Wallow and Public View areas, and elephants had longer bouts near the Building, Door, Water Source, Trees, and overall.

Elephants: Increased temperature corresponded to increased time spent near the Trees and less time near the Building; there were no changes in other exhibit locations. Substrate choices mirrored exhibit area changes, with dirt use increasing and cement use decreasing with rising temperatures.

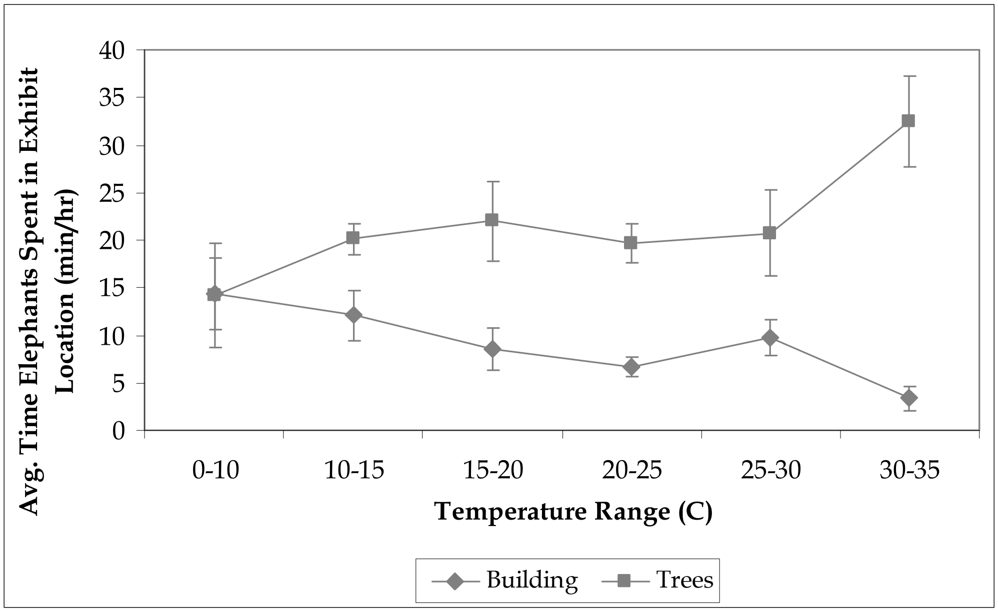


Figure 8. Temperature-related trends in exhibit location in elephants. Subjects spent more time in the Tree area and less time in the Building area with increasing ambient temperatures.

Elephants were near the Building more often on overcast days than sunny/cloudy days (13.34±0.96 vs. 8.78±0.08 min/hr). Water usage also varied with weather conditions, with more time spent near the water source on sunny days than cloudy/overcast days (21.69±3.12 vs. 17.25±0.64 min/hr).

Rhinos: Rhinos increased time spent in the Tree area with increasing temperatures, though with more variability than the elephants, and spent less time near the water source. Rising temperatures were also associated with increased time in the Public View Area and decreased time near the Door, but neither change was significant. Mud substrate was used significantly more often at temperatures below 15°C than at higher temperatures (37.32±4.32 vs. 7.31±1.48 min/hr), and Dirt was used significantly less often at temperatures below 15°C

(21.32±4.35 vs. 48.89±1.36 min/hr). There were no changes in exhibit use corresponding to weather conditions.

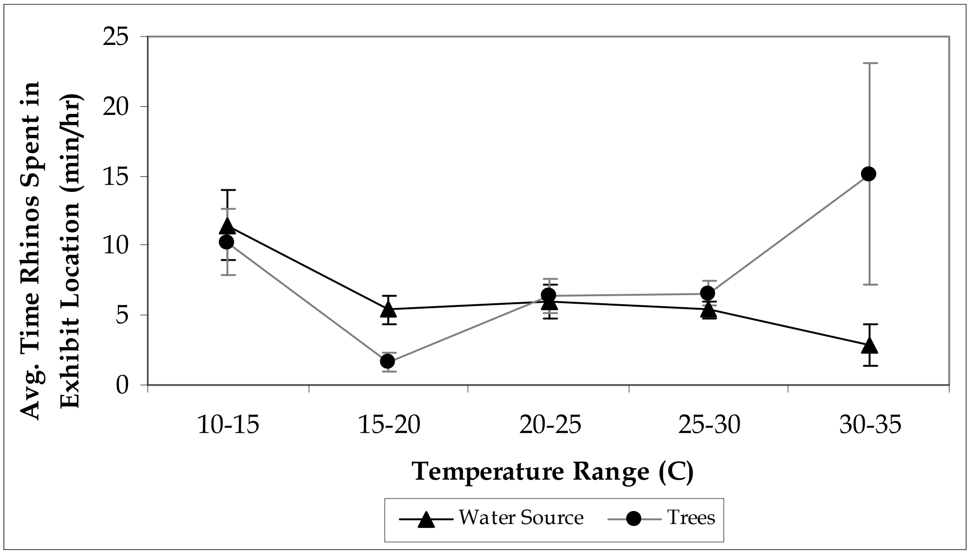


Figure 9. Temperature-related trends in exhibit location in rhinos. Subjects spent more time in the Tree area and less time in the Water Source with increasing ambient temperatures.

Discussion

Object Exploration: Subjects were expected to increase object investigation when outside due to the larger and more diverse environments of the outdoor enclosures, and the results supported this in both species. Elephants are known to be attentive to their environment and will rarely leave novel objects unexplored (Adams & Berg, 1980). Object investigation consists of multiple behaviors directed toward something within the environment; it may include sniffing, picking the object up with the trunk, manipulating the object, or even tossing the object. The elephants averaged only 5.79±1.62 min/hr investigating objects in the indoor enclosure with bouts of only 12 seconds, but when housed outside both the total time investigating and the average bout length doubled.

This is likely because of both more opportunities for exploration and an increased motivation to explore the given environment: when housed inside elephants are limited to mostly investigating the building walls and substrate, but outside there is more environmental variability that includes rocks, trees, logs, and multiple substrates to explore. The rhinos spent less time investigating objects than the elephants but did display the behavior more outside and in conjunction decreased resting. Little information is available relating to object exploration in black rhinos either in captivity or in the wild, but the species has natural activity levels much lower than that of elephants (Estes, 1991; Kiwia, 1986; Schenkel & Schenkel-Hulliger, 1969) and therefore lower levels of investigation would be anticipated.

Environmental exploration is important to many species and lack of opportunity or motivation can negatively affect activity budgets; captive enclosures should include environmental features that encourage investigation and provide behavioral outlets, especially in otherwise barren spaces (Carlstead, 1996; Carlstead et al, 1993; Veasey, 2006). Properly designed enclosures can also decrease abnormal behaviors: carnivores housed in enclosures containing physical objects and structures that encouraged investigation have shown more natural behaviors and fewer stereotypies than those housed in barren environments (e.g. Carlstead et al, 1993; Mallapur et al, 2002). The elephants displayed fewer abnormal behaviors in the outdoor enclosure, and investigation (environmental and enrichment) was the only behavior to increase in opposition.

For elephants, having objects and substrates with which they can interact provides the opportunities for environmental manipulation and exploration that they would normally be engaged in when moving and foraging in the wild. This is also true for rhinos; although less explorative than elephants in this study they did display the behavior and natural levels of investigation should be encouraged using proper exhibit design. Captive enclosures, both outdoor and indoor, should be designed with the behavioral needs of each species in mind, providing animals with the opportunity, motivation, and choice to investigate the environment. Enclosure design may actually be more influential on animal behavior than just the size of the space (Carlstead, 1996; Frézard & LePape, 2003; Morgan & Tromborg, 2007), and in cases when the space is already restricted, such as in many indoor enclosures, appropriately outfitted environments may help prevent anxiety and boredom in elephants and rhinos (Carlstead et al, 1993). The results suggest that elephants and rhinos would benefit from objects that stimulate investigation and are able to be manipulated, including logs and branches (for carrying, tossing, pushing, and stripping bark) and soft substrates (for bathing and digging). Non-naturalistic items can also promote investigatory behaviors, such as food dispensers that require animals to manipulate the object in order to obtain the food. These types of objects may be advantageous if integrated into the design of both outdoor and indoor exhibits for these species.

Rhino Scent Marking: Although black rhinos are not territorial, individuals inhabit home ranges that are shared by other rhinos and urinary scent marking is a common species behavior. Ritualized urination is more commonly seen in males than females (Carlstead et al, 1999a; Hutchins & Kreger, 2006; Schenkel & Schenkel-Hulliger, 1969), and Jimma urine sprayed at over three to four times the rate of either female in either enclosure. His rate was significantly greater when housed inside, which was not expected and may be due to the closer proximity of the females. The scent of the females would be present in the outdoor enclosure, which would encourage scent marking, and the behavior is also common during environmental investigation and patrolling of their home ranges (Schenkel & Schenkel-Hulliger, 1969). However, the immediate proximity of the females may be a greater influence than just scent, as social and sexual interactions also stimulate the behavior (Schenkel & Schenkel-Hulliger, 1969).

High levels of urine spraying inside are also hypothesized to be due to captive cleaning practices. Carlstead et al (1999b) found that higher frequencies of olfactory behaviors (urine spray and anogenital/urine/feces investigation) and stereotypy were correlated with increased chlorine use at the housing institution, and the authors suggested that disturbing the natural olfactory environment of black rhinos may result in arousal and agitation, especially in males. The indoor rhino enclosure at CMZ was disinfected approximately twice per week, and the male did perform urine sprays and stereotypic behavior significantly more often than the females. This disparity may represent sexual differences in coping with a disturbed olfactory environment (Carlstead et al, 1999b). Routine cleaning practices can interfere with chemical communication by erasing conspecifics odors and can significantly affect behavior in species that rely primarily upon scent cues (Berkeley et al, 1997; Maple & Perkins, 1996; Morgan & Tromborg, 2007). Olfaction is a primary sense in black rhinoceroses, which use urine and fecal scent marks throughout their home ranges to assert their own presence and identify other individuals within the area (Schenkel & Schenkel-Hulliger, 1969). Whether traditional cleaning routines in captivity cause increased levels of stress is unclear, but future studies specifically linking the practice of enclosure cleaning with changes in rhino behavior and stress hormone levels would be beneficial in clarifying this relationship.

Rubbing: Rubbing and scratching act to remove dead skin (Hutchings & Kreger, 2006). Both elephants and rhinos used objects within their environment to rub and scratch their bodies; rhinos rubbed more than elephants, and both species rubbed more when inside than when outside. Excessive rubbing is often thought an appetitive behavior performed out of boredom or frustration (Maple & Perkins, 1996; Schenkel & Schenkel-Hulliger, 1969), and the increased rubbing seen inside may be due to lack of other behavioral opportunities or anticipation of food due to keeper presence. However, average levels were less than three min/hr and the subjects were never seen injuring themselves, so it is unlikely the behavior can truly be deemed excessive. When inside both species most often rubbed against the walls and bars of the buildings, as these were the most prominent available structures; elephants also rubbed against the building most when outside. Although these hard substances can be effective in removing dead skin and stimulating nerves, especially from the sides and rump, they should not be the only structures available to elephants and rhinos. In the wild these species use their tusks and horns, respectively, for foraging and browsing, and actions such as tearing apart foliage and stripping leaves bark help to naturally wear down the armaments. These types of materials were not often available inside, and rubbing tusks and horns on hard surfaces such as the building interior can lead to injury (Maple & Perkins, 1996); both adult rhinos had previously injured their horns by rubbing on bars and doors within their indoor enclosure. Since providing constant browse material is not probable in captivity, elephants and rhinos may benefit from having alternative objects of softer materials, either natural or artificial, within their indoor enclosures. The rhinos, for instance, most often rubbed against logs and wooden scratching posts when outside and may therefore prefer these softer items when they are available. Captive enclosures need to provide species-specific structures that can be used for rubbing, especially in large ungulates that cannot otherwise scratch their bodies (Adams & Berg, 1980; Maple & Perkins, 1996). Future studies that examine animal preferences and physical effects of harder versus softer objects would help determine how best to manage this behavior.

Elephant Abnormal Behavior: The elephants engaged in more abnormal behavior when housed inside, as has been seen in other studies of captive ungulates (e.g. Bashaw et al, 2001; Elzanowski & Sergiel, 2006). Captive feeding methods relying upon concentrated, easily eaten food are often blamed for stereotypies in ungulates (Bashaw et al, 2001; Morgan & Tromborg, 2007), but hay was present throughout the day in this enclosure. Additionally, oral stereotypies are most commonly associated with feeding frustration in ungulates (Bashaw et al, 2001; Bergeron et al, 2006), but locomotor stereotypies were more prevalent in the elephants. These results suggest that the abnormal behaviors were due to factors unrelated to feeding (Bashaw et al, 2001; Mason, 1991). Given the prevalence of the behavior inside it is likely the physical surroundings were a factor: the indoor enclosure was smaller and more barren, providing fewer opportunities for locomotion, investigation, and object manipulation. Small, unstimulating environments are often associated with chronic stress and stereotypies, especially locomotor behaviors such as weaving and pacing (Bashaw et al, 2001; Carlstead, 1996; Mason, 1991). Bashaw et al (2001) found that captive giraffe and okapi were significantly less likely to pace if they were housed in larger indoor enclosures or had experienced an environmental change in the past year, suggesting increased space and environmental variety may reduce the performance of locomotor stereotypies in ungulates. Asian and African circus elephants significantly decrease the performance of stereotypic behavior when kept in pens or paddocks versus chains or pickets (e.g. Friend & Parker, 1999;

Gruber et al, 2000). In this study the elephants did not locomote less inside, but did have lower levels of environmental interaction and investigation during the winter months; this suggests that novelty and investigatory opportunities are likely as important as adequate space when elephants are housed inside. Consistently varying indoor enclosures is not a feasible solution for zoo-housed elephants, but increasing available space and providing more diverse enrichment items within the indoor enclosure is. Although established stereotypies are highly resistant to change and the addition of space or enrichment items will not always reduce their occurrence (Lukas et al, 2003; Maple & Perkins, 1996), if the solutions address the underlying motivation behind the behavior it is possible to increase the welfare of the animals irregardless of the eradication of the abnormal behaviors (Mason et al, 2007). Cross-institutional work assessing enclosure size and design in relation to behavior would be useful in determining if these factors influence the performance of abnormal behaviors in elephants.

When housed outside the average time the elephants displayed abnormal behavior was greater in colder weather, which has also been documented in Asian elephants (Rees, 2004). Temperatures within the African savannah can drop below freezing, and although elephants do not cope with these ranges for extended periods of time it is unlikely the elephants at CMZ were physically stressed when outside during the day in 0-10°C temperatures (Rees, 2004). It is possible, however, that the colder weather is more uncomfortable and the increase in abnormal behavior was due to a desire to return to the indoor enclosure. The increase in abnormal behavior could also be due to an unmeasured or undetectable environmental or social variable, and not directly related to the ambient temperature (Rees, 2004). Further work relating the performance of stereotypic behavior in relation to temperature and weather would be beneficial for zoos in northern climates. Establishing preferable temperature ranges for elephants housed outside could be used to modify husbandry procedures and improve captive elephant welfare.

Enrichment: Both species displayed longer investigatory bouts with Natural and Food enrichment than with Artificial, suggesting these items were more stimulating. These types of items were more often given to the elephants in the outdoor enclosure, which was associated with decreased resting, increased social behavior, and more overall enrichment use than the indoor enclosure. Stoinski et al (2000) found that providing browse to elephants when outside decreased resting behavior and also increased time spent feeding, resulting in a more natural activity budget; browse may also increase locomotory behavior when spread throughout the enclosure (Veasey et al, 1996). Browse takes more time to eat than similar amounts of hay or concentrated grains, occupying animals for longer periods of time while also encouraging natural foraging behaviors; it is an effective enrichment item for captive elephants and rhinos, but not the only possibility. Any novel items that stimulate interest and investigation in animals can potentially increase activity, natural exploratory behaviors, and overall behavioral options (Morgan & Tromborg, 2007). This often makes enrichment useful in reducing abnormal and appetitive behaviors in captive ungulates, as it can provide a means of behavioral expression and in environments that are otherwise barren, unstimulating, or stressful (Mason et al, 2007; Swaisgood & Shepherdson, 2005). Enrichment items are, however, only effective if used by the animals to which they are presented, and enrichment programs should focus more on the effectiveness of an item than its availability and ease of implementation. For example, Artificial enrichment items are typically long-lasting and easy to implement and thus are commonly used in zoos. These can be beneficial in providing novelty and the opportunity to perform different behaviors, but if the same few items are repeatedly presented to an animal it can lead to habituation and diminished usage (Carlstead, 1996). Variability and novelty are therefore crucial but often overlooked components of enrichment programs (Morgan & Tromborg, 2007).

Novelty is important in stimulating exploration and manipulation in animals and enrichment programs should employ multiple different items within multiple enrichment categories. Animal managers could then rotate what type of and specific items are presented to animals, increasing the effects of novelty and decreasing lack of interest due to monotony. In the wild both elephants and rhinos feed on numerous species of plants with many different textures and flavors (Estes, 1991); providing various types of food enrichment that differ from the daily feeding regimen may stimulate interest in foraging behaviors. Both species also reside in dynamic environments in the wild and may benefit from exposure to various substrates, odors, or other natural materials that encourage manipulation and exploration. Altering enclosures, which provides environmental novelty, increased enclosure use and feeding behavior in two groups of captive gorillas, and activity levels were higher in the novel environment (Lukas et al, 2003). Providing multiple enclosures for larger animals such as elephants and rhinos is not practical for most zoos, but creating novel spaces by varying enrichment items and environmental objects may have similar effects. Future studies could focus on how the behavior of elephants and rhinos is affected by regular environmental changes due to novel enrichment items.

Enrichment for captive elephants and rhinos can clearly come from many sources, including physical objects, feeding methods, sensory stimulation, and even interactions with conspecifics and humans; husbandry programs that provide multiple forms of enrichment from multiple categories will ensure continued novelty. Multi-institutional studies examining enrichment preferences among elephants and rhinos may help to identify different types of items that can easily be used in zoos and are effective in encouraging more natural behaviors. Individual penchants for specific enrichment items will limit species-wide conclusions of what items may increase activity and natural behaviors, but research of animal preferences can help construct general principles that could thereafter be modified based on individual needs (Swaisgood & Shepherdson, 2005).

Exhibit Use: Elephants and rhinos both spent more time near the Building and Door of the exhibits than was expected based upon area size, and less time near the Public View Area. Subjects were often observed near the Building or Door prior to scheduled shift times, and these areas were also where the majority of all outdoor abnormal behaviors occurred in both elephants and rhinos. Elephants in zoos and circuses often increase the performance of stereotypic behaviors prior to daily scheduled events such as feeding (e.g. Friend, 1999; Gruber et al, 2000; Rees, 2004; Wilson et al, 2004). This suggests that the elephants and rhinos may have utilized the Building and Door areas due to an anticipation or desire to enter the indoor enclosure. Although the use of these areas was higher than expected it is not necessarily unfavorable; subjects did not spent the most overall time in these areas but instead more frequently utilized other parts of the exhibit. The low use of the Public View Area was anticipated in the black rhinos, which as a species are often averse to or afraid of humans (Schenkel & Schenkel-Hulliger, 1969) and therefore unlikely to frequent the exhibit area closest to zoo visitors. The elephants may have avoided this area for similar reasons or because of the area's different environmental features. It had a grass substrate and was adjacent to the moat surrounding the exhibit perimeter; the animals may have preferred the dirt substrate comprising most other exhibit areas or purposefully avoided the moat. The Public View Area was the closest to zoo visitors but animals were highly visible in all areas of the exhibits. Decreased use of this particular area is therefore not necessarily undesirable but may actually have the benefit of allowing the elephants and rhinos to control their proximity to zoo visitors without affecting visibility.

Species differences were seen with the Wallow and Tree areas, the former favored by rhinos and the latter by elephants. The results of the Wallow area were as expected based on the species' natural behaviors: rhinos use mud wallows as a primary means of heat dissipation and protection from the sun and insects (Hutchins & Kreger, 2006). The high use of the Trees by the elephants could be due to a number of factors. It provided more shade than other exhibit areas and contained a large rock the elephants used for rubbing, both of which may have caused increased usage. The trees may have been stimulating as well; although the elephants could not reach the trees themselves due to protective fencing they were often seen reaching their trunks through the fence to investigate the substrate and pick up objects.

When temperatures rose above 30°C the elephants increased their time in the Tree area and decreased time near the Building, and use of the Building area was lower on sunny days than cloudy or overcast days. The Building area contained a cement substrate and no shade; moving to the Tree area would provide the elephants with shade and a substrate that was both cooler to stand on and allowed for dusting. The rhinos also used the Tree area more as temperatures rose above 15°C, along with a slight increase in use of the Public View Area; these two areas provided more shade than other areas of the exhibit. The increased use of shaded areas by both species highlights the need for outdoor exhibits to provide adequate shade structures. Exhibit design should account for possible sun exposure and increasing ambient temperatures and ensure that all individuals have the opportunity for shade and cool substrates when desired.

Pools were available to both species but individuals were rarely seen in the water; the elephants were never seen in the water when the pool was filled, and the female rhinos entered the pool on only one occasion. Adams & Berg (1980) reported similar results in a study of captive elephants and hypothesized that it may be due to the lack of multiple water sources. Anecdotal field observations have noted that elephants may prefer to maintain separate drinking and swimming sites (Adams & Berg, 1980); in both the elephant and rhino enclosure the pool was the sole water source available to the animals. Future studies could examine the use of bathing sites by these species in enclosures with one versus multiple water sources to determine if providing a separate bathing site encourages increased use of the water. It is also possible that the daily and semi-daily baths given by the keepers were sufficient for the bathing needs of the animals, or that the animals entered the pool during times data were not being collected.

Zoo enclosures cannot replicate the African savannahs that are the natural habitats of African elephants and black rhinos, but they can for most species provide enclosures of adequate space and complexity to allow increased choice and control and thus promote natural activity levels and behaviors (Frézard & Le Pape, 2003; Mallapur et al, 2002). Natural behavior is an important aspect of determining proper enclosure specifications and research linking behavior and exhibit use and design should be encouraged to continuously improve zoo standards (Hutchins & Kreger, 2006). Size is, of course, a primary consideration. Veasey et al (1996) found that larger enclosures were associated with increased locomotion and rumination in giraffes, both important species-typical behaviors that should be encouraged in captivity. Size is additionally important in relation to social groups; increased social densities are correlated with decreased reproduction and reduced life spans in both African elephants and black rhinos (Price & Stoinski, 2007). Exhibit design is equally important, as animals are more likely to display natural behaviors in surroundings similar to their natural habitats (Maple & Perkins, 1996). For elephants and rhinos, this means the inclusion of items such as scratching posts, mud wallows, natural substrates, shade structures, and pools (Maple & Perkins, 1996). Appropriate physical objects, enrichment items, foraging opportunities, and space for locomotion all contribute to the overall complexity of the environment and help to provide sensory stimulation and behavioral opportunities for captive animals (Carlstead, 1996). Providing numerous choices as to spaces and activities and thereafter allowing animals to choose when and how to use these resources gives animals some control over the environment, a quality that is inherently lacking in captivity but important for psychological health and well-being (Carlstead, 1996; Frézard & LePape, 2003).

Summary and Conclusions

1. Elephants decreased object exploration and increased abnormal behavior inside, suggesting they would benefit from more environmental diversity and behavioral options in the indoor enclosure.
2. The male rhino urine sprayed significantly more inside. Future studies should examine how this behavior relates to the presence of other individuals and/or captive cleaning and disinfecting practices.
3. Both elephants and rhinos rubbed more when housed inside, which may be due to lack of behavioral opportunities or displacement. Indoor enclosures should provide a variety of natural objects for elephants and rhinos to use for rubbing their tusks, horns, and heads in order to prevent injury.
4. The elephants and rhinos utilized Natural and Food enrichment items for greater amounts of time than Artificial items. Captive institutions should consider individual animal preferences and novelty when designing enrichment programs, and should evaluate usage to determine which items are most effective.

5. Outdoor enclosures for elephants and rhinos should contain adequate shade structures, environmental objects, and a variety of substrates. Future work examining water use would help determine if animals are more likely to utilize pools for swimming when given separate drinking sources.

Chapter 3: Social Dynamics and Abnormal Behaviors in African Elephants and Black Rhinoceroses Housed at Cleveland Metroparks Zoo

Introduction

Maintaining functional social groups in captivity is a primary welfare concern (Frézard & LePape, 2003; Veasey, 2006), and a better understanding of how African elephants and black rhinos interact with conspecifics in captivity will result in more informed decisions regarding social housing and management. Social groups are an effective and long-term form of enrichment that can provide captive animals with increased behavioral opportunities and a more dynamic environment (Veasey, 2006). Most ungulate species can adapt to various social situations (Veasey, 2006), but if group structures differ from what is seen in the wild behavioral research can help determine whether those groups are providing animals with their social needs while preventing high levels of social tension. African elephants and black rhinos are two species that are often housed in unnatural social groups in captivity. African elephants in the wild live in matriarchal herds composed of related females and their offspring, but in captivity elephants are typically housed in small groups of unrelated females (Hutchins, 2006; Olson & Wiese, 2000; Schulte, 2000). Black rhinos are solitary as adults, but many zoos house this species in pairs or small groups, and may house both males and females together (Carlstead & Brown, 2005; Hutchins & Kreger, 2006). Despite this, both elephants and rhinos have been successfully housed in captivity, suggesting that group composition and compatibility have a significant impact on how these species adapt to unnatural social groups. Social stability results in predictable behaviors from all individuals and low levels of social aggression and stress (Heitor et al, 2006a; Sachser et al, 1998; Wilson et al, 2006). Ensuring stable social relationships within groups of elephants and rhinos should therefore be a priority for captive population management programs.

In addition to unnatural social groupings, captive elephants and rhinos must also adapt to different environments. Captive enclosures present many biotic and abiotic stimuli that would not be encountered in the wild (Carlstead, 1996). Also, enclosures and management procedures can interfere with the behavioral needs of some animals, including feeding, locomotory, and social behaviors (Gruber et al, 2000; Morgan & Tromborg, 2007). The lack of control animals have over these environmental variables can often result in the development of abnormal behaviors. Abnormal behaviors are not desirable in zoos, as they may indicate compromised animal welfare and present a negative image to zoo visitors (Mason et al, 2007). High levels of abnormal behaviors are also associated with lower levels of natural behaviors and thus result in atypical activity budgets (Gruber et al, 2000); this diminishes the ability to apply behavioral knowledge gained to other captive or wild populations (Mason et al, 2007). Abnormal behaviors can be difficult to eliminate in captive animals because of habitual performance, but the best method of addressing them is to first understand the underlying motivation of the behavior (Mason, 1991; Mason & Latham, 2004). Individual animals vary in both the development and performance of abnormal behaviors; this idiosyncratic nature makes it difficult to generalize possible motivational factors and potential methods of reducing the performance (Mason, 1991). Even within the same environment individuals will perform different types of abnormal behaviors and some individuals will not display any; this suggests that individuals do not adapt to captivity in the same way (Mason, 2006a). Studies of abnormal behavior that focus on individual animals and include not only behavioral analyses but also individual histories and environmental and social variables can be useful in providing a clearer understanding of the behaviors.

The purpose of this study was to evaluate the social organization andexamine individual differences in the behavior of three female African elephants and one male and two female black rhinoceroses. The objectives were to establish the levels of aggression and affiliation within each group, the presence or absence of a social hierarchy, and how the performance of abnormal behavior differed within each species. Although this study investigates the behavior of only one group of each species, the results demonstrate the importance of evaluating individual differences when determining how each captive group of elephants and rhinos can best be managed.

Methods and Materials

Subjects: Please refer to Chapter 1 Methods and Materials for information on subjects, management, and housing.

Data Collection and Analysis: Please refer to Chapter 1 Methods and Materials for data collection and analysis protocols.

Results

Elephant Social Behavior: Elephants averaged 0.75±0.12 min/hr of total social behavior, with no difference between enclosures. Jo was engaged in dominant/submissive interactions significantly more than Moshi or Tika, and was the only individual to not show a significant difference between this and affiliative behavior. Tika was engaged in affiliative behavior slightly more often than the other elephants. There were no individual differences in other social behavior.

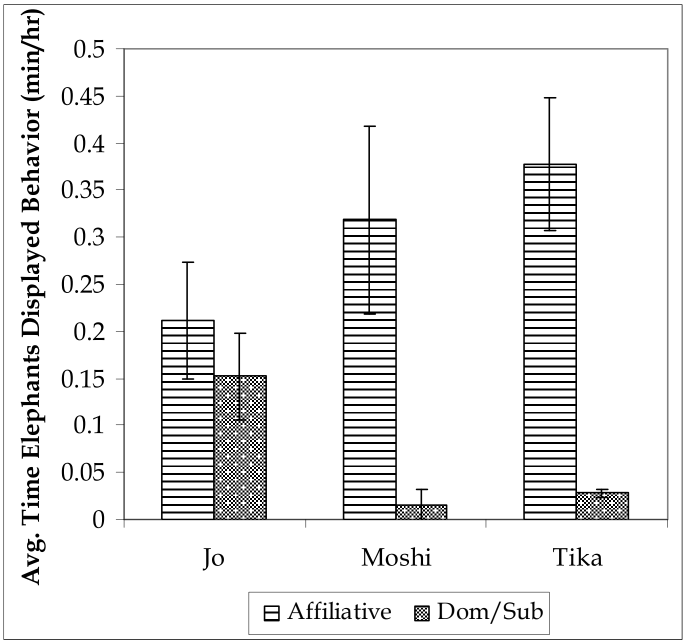


Figure 1. Mean time displaying social behaviors. Moshi and Tike had similar levels of both affiliative and dominant/submissive interactions. Jo showed less affiliative behavior and more dominant/submissive behavior than the other elephants.

Jo engaged in Affiliative interactions significantly more when outside. Moshi and Tika averaged more social behavior inside, though the changes were not significant. When housed inside Jo increased locomotion and object investigation when solitary versus with Tika.

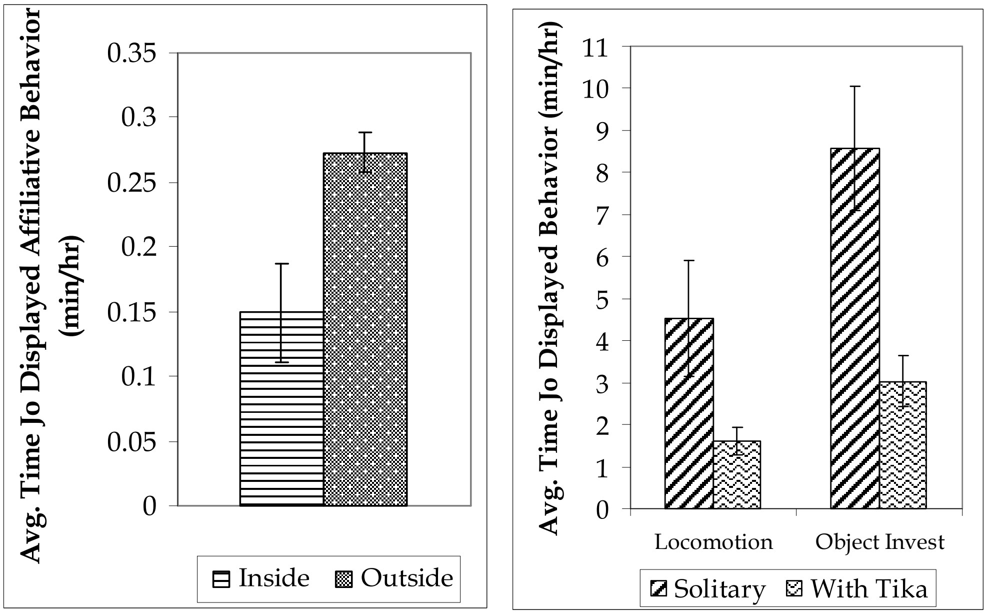


Figure 2. Social behavior in Jo in relation to enclosure (A) and indoor social housing (B). Subject engaged in more affiliative interactions when housed outside. When housed inside, subject increased locomotory and investigatory behavior when housed solitarily.

Tika showed greater amounts of affiliative and other behavior when housed inside with Moshi than with Jo, and also spent less time eating when housed with Moshi.

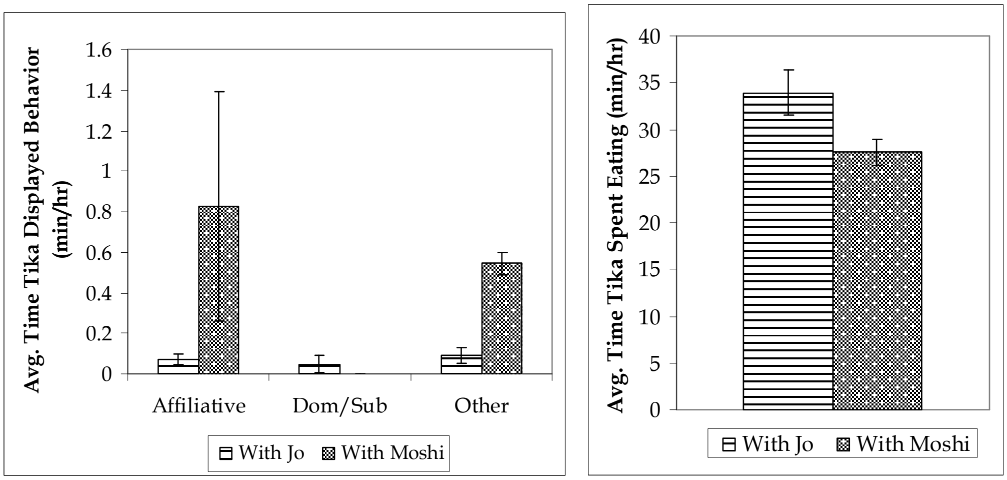


Figure 3. Effects of housing companion on social behavior (A) and eating (B) in Tika. Subject increased affiliative and other social behaviors and decreased eating when housed with Moshi.

Jo displaced Tika on multiple occasions in both the outdoor and indoor enclosures. Following a displacement, Jo had the highest probability of eating (0.33±0.13%) or investigating an object or enrichment item (0.25±0.16%). On only one occasion did Tika display submissive behavior after being displaced. Neither Moshi nor Tika were observed displacing another elephant.

Social interactions, including approaches and leaves, are important for establishing social relationships, and each elephant differed in the number of interactions she initiated with the two other females. Jo directed much more affiliative behavior toward Tika than toward Moshi and more than Tika directed to Jo. She approached the other elephants more than she left them and more than they approached her. Moshi initiated affiliative behavior only toward Tika and submissions only toward Jo, and left Jo more often than approaching her. Tika directed more affiliative behavior toward Moshi and more submissions toward Jo. She had slightly fewer approaches than leaves with Jo, and fewer leaves than approaches with Moshi; neither of these were significant.

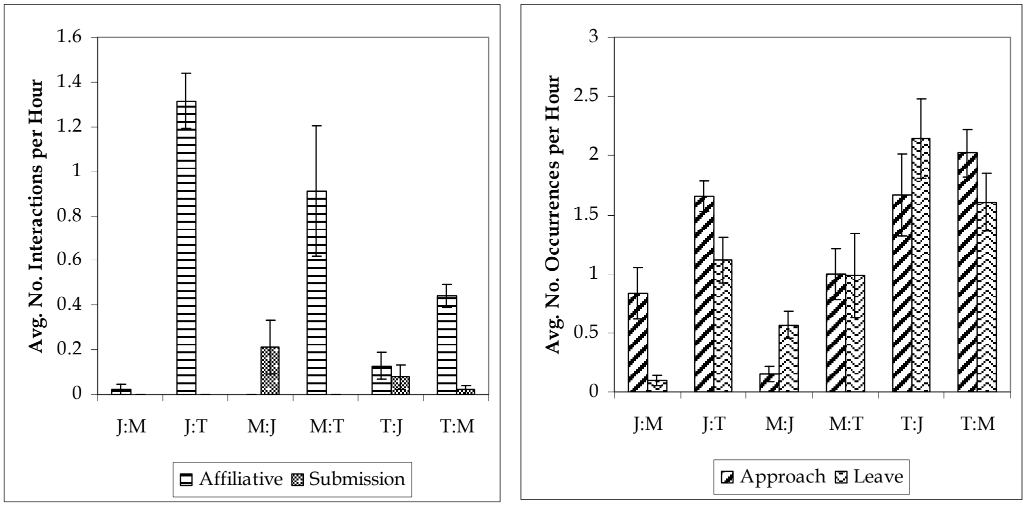


Figure 4. Rate of social interactions (A) and approaches/leaves (B) when housed outside. Data presented as **initiator:recipient**; J=Jo, M=Moshi, T=Tika. Data include only interactions initiated by the subject. Jo rarely received affiliative behavior and was never submissive. Moshi was very submissive to Jo. Tika received more affiliative interactions from both other elephants than she initiated and was submissive to both Jo and Moshi.

Elephant Abnormal Behavior: Each elephant displayed different types and proportions of abnormal behaviors (Table 1).

Table 1: Individual Performances of Abnormal Behavior in African Elephants

Inside	Sway	Pace	Bob	HB	SS	Agg
Jo	95.5	3.5	-	1	-	-
Moshi	-	-	99.5	-	0.5	-
Tika	-	50	-	-	46	4
Outside						
Jo	19.7	80	-	0.3	-	-
Moshi	0.19	-	0.79	0.02	-	-
Tika	57	-	-	-	41.5	1.5

Data are presented as percent time performing each type of behavior in relation to total performance of abnormal behavior in the given enclosure.

Average time spent in abnormal behaviors was greater in the inside enclosure in all individuals. Tika showed the least amount, while Jo's performance was highly variable. Jo showed a disparity in relation to social housing in the inside enclosure, averaging over nine times the amount of abnormal behavior when with Tika than when alone.

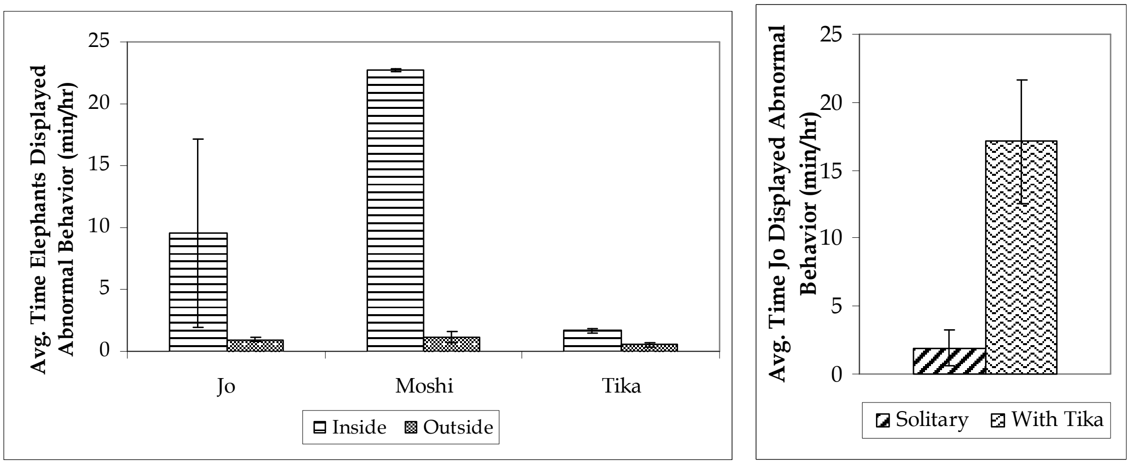


Figure 5. Performance of abnormal behaviors in relation to enclosure (A) and social housing in Jo (B). All subjects performed abnormal behaviors more often inside, and Jo performed abnormal behaviors more often when housed with Tika than when alone.

Rhinoceros Social Behavior: The male rhino was housed solitarily outside and thus no outside social behavior data were available. The female rhinos averaged 0.37+0.02 min/hr of total social behavior when housed outside, with no difference between individuals. All rhinos averaged 1.45±0.20 min/hr of total social behavior when housed inside, also with no difference between individuals. When grouped by sex and age, however, differences were apparent in all four social behavioral categories. The females showed greater average time in agonistic and other behavior than the male, and the adults displayed more affiliative and sexual behavior than the juvenile.

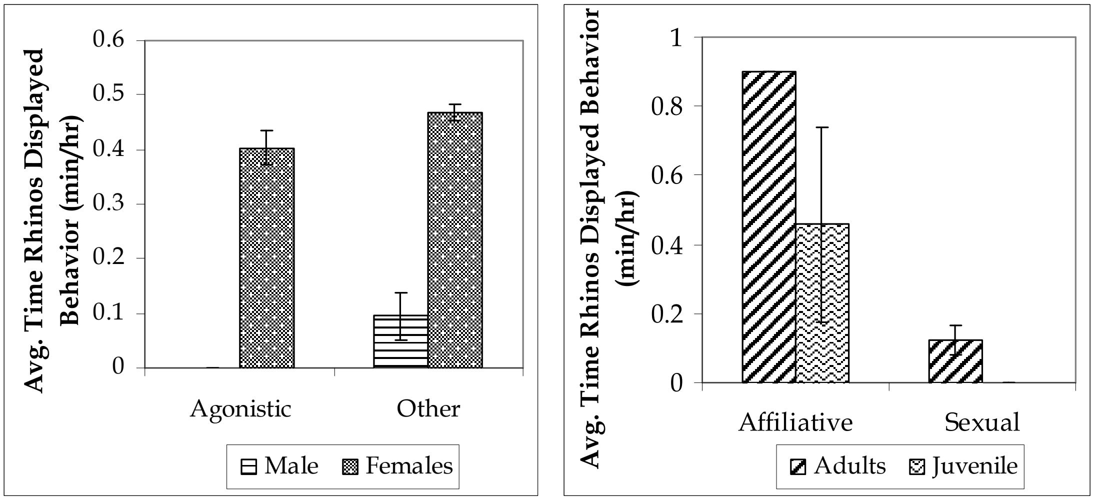


Figure 6. Mean time spent displaying social behavior in relation to sex (A) and age (B). The female rhinos displayed significantly more agonistic and other behavior than the male, and the adults displayed more affiliative and sexual behavior than the juvenile.

Agonistic behavior between the female rhinos was rare but did occur both inside and outside. The behaviors seen included horn and head butting, mock charges, and pushing, and never resulted in injury to the individuals. The encounters were initiated by both individuals and usually involved several individual bouts (avg. 54.68±21.2 sec). No known husbandry or managerial changes preceded these incidents and no abnormal behaviors were recorded on those days.

Specific social relationships were only investigated between the two female rhinos. Affiliative behaviors were more commonly directed from Kibibbi toward Inge. No dominant or submissive displays were recorded, but multiple displacements by both females were seen. Inge only displaced Kibibbi in the inside enclosure and only initiated affiliative behavior with her outside. She was also more likely to leave Kibibbi than approach her. All but one of Kibibbi's displacements of Inge were outside and she initiated affiliative behavior in both enclosures; she approached Inge more than she left her. Approaches were rarely followed by social behavior (8±3%), but all interactions that did result were affiliative. Displacements had a high probability of being followed by resting (60±24%)

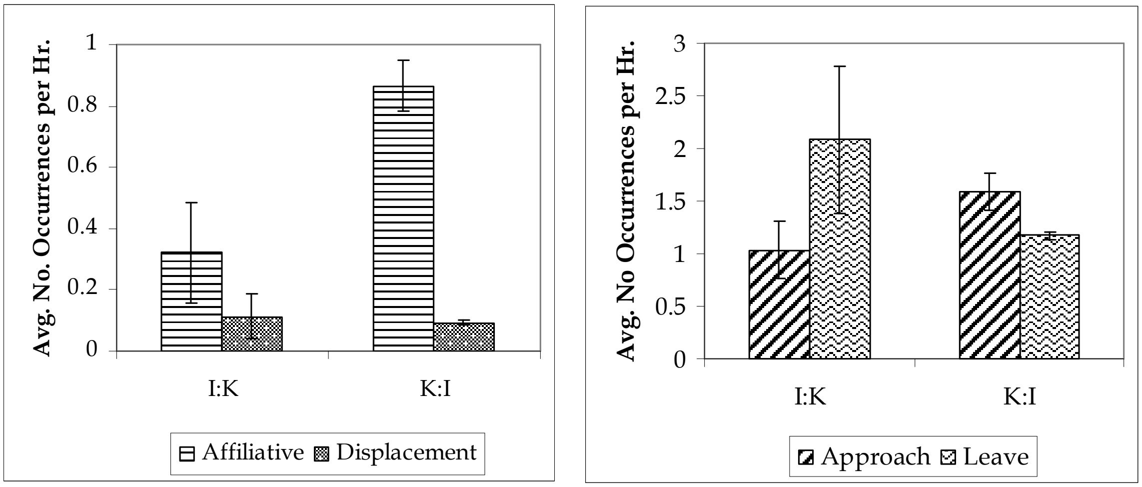


Figure 7. Rate of social interactions (A) and approaches/leaves (B) when housed outside. Data presented as **initiator:recipient**; I=Inge, K=Kibibbi. Data include only interactions initiated by the subject. Kibibbi initiated more affiliative interactions than Inge; subjects had similar rates of displacements.

Rhinoceros Abnormal Behavior: As was seen in the elephants, each rhino displayed different types and proportions of abnormal behaviors (Table 2).

Table 2: Individual Performance of Abnormal Behavior in the Rhinos

Inside	Sway	Pace	HB	Agg	Mth
Jimma	1.5	97	1.5	-	-
Inge	-	91	-	-	9
Outside					
Jimma	0.3	99	0.7	-	-
Inge	-	0.49	0.04	0.47	-
Kibibbi	-	-	10	81	9

Data are presented as percent time performing each type of behavior in relation to total performance of abnormal behavior in the given enclosure.

The rhinos overall displayed less abnormal behavior than the elephants and tended to display more outside. Kibibbi showed none inside and averaged less than 0.01 min/hr outside, and Inge averaged only about one min/hr both inside and outside. Jimma showed the most abnormal behavior but his performance was highly variable depending on the environment, with a significantly higher rate in the front yard than the back yard or inside. There were no differences between AM and PM hours, temperature, or weather.

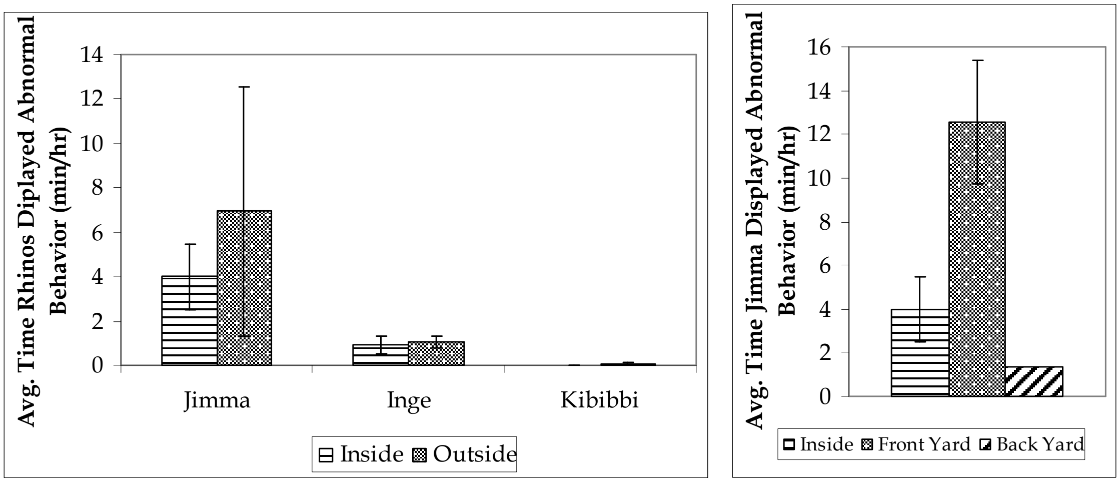


Figure 8. Performance of abnormal behaviors in relation to enclosure in all rhinos (A) and Jimma (B). Female rhinos had low and invariable rates of abnormal behaviors. Jimma did not differ in performance inside versus outside, but displayed significantly more abnormal behaviors in the front outside yard than either the back outside yard or inside.

Discussion

Elephants: The most common social behaviors seen in the elephants were species-typical affiliations. Trunk-to-mouth greeting behavior was the most frequently occurring social behavior, as was also noted by Adams & Berg (1980); it was seen between all individuals. It is often seen following an approach or when two individuals pass each other or walk together; usually it is reciprocated or performed simultaneously (Adams & Berg, 1980; Estes, 1991). The behavior is thought a gesture of friendship akin to a human handshake, but may also be used to soothe a restless elephant, prevent aggression from a more dominant individual, or gain information on what another has eaten or drank (Adams & Berg, 1980; Garaï, 1992). Another affiliative behavior was intertwining trunks, which is most common in younger elephants and often considered a play behavior (Adams & Berg, 1980). Elephants may also caress another individual by placing and/or rubbing the trunk across the head, neck, or back, which is thought reassuring for both individuals (Adams & Berg, 1980; Garaï, 1992). Both of these behaviors are examples of the importance of physical contact in elephant sociality. Tika displayed these behaviors with Jo and Moshi, suggesting she had a friendly relationship with both other elephants. Jo and Moshi were never seen displaying these behaviors, which emphasizes their primarily antagonistic relationship. Tika, the youngest elephant, was involved in the most affiliative behavior overall and was more often the recipient than the initiator. Garaï (1992) noted a similar phenomenon in a group of Asian elephants, with the youngest being a 5-year-old with no kin in the group. Tika's younger age may thus have influenced her friendships with both Jo and Moshi, but as all individuals were adults this could also have been due to individual social preferences.

Overt aggression was rarely seen amongst the elephants at CMZ, and low rates of female aggression are common in both captive and wild groups of elephants (e.g. Archie et al, 2006; Adams & Berg, 1980; Brockett et al, 1999; Garaï, 1992; Gruber et al, 2000; Wilson et al, 2006; Wyatt & Eltringham, 1974). Play fighting, including mild trunk wrestling, tusking, and pushing, was only seen between Moshi and Tika and is thought to maintain the hierarchy without necessitating dangerous and energetically costly fights (Brockett et al, 1999). Adams & Berg (1980) noted that play fighting was only seen between certain pairs of elephants; it is likely that Jo was never seen engaged in this due to her stable position as dominant female.

Social animals such as elephants maintain stable hierarchies as a means of decreasing aggression among herd mates (Buss, 1990). Stable social relations among wild elephants are maintained by the matriarch, generally the eldest group member. She is responsible for leading the herd to necessary resources and sustaining social accord within the group and with other groups, though the degree to which a matriarch does so can vary (Estes, 1991; Vidya & Sukumar, 2005). In captivity elephants are provided with necessary resources and most duties of a matriarch are unnecessary; experience and knowledge are therefore not as vital for the leader to possess, and hierarchies among captive female elephants are not necessarily age-based (Garaï, 1992). Instead, the most behaviorally dominant female within a captive group will often take over the role of social leader (Schulte, 2000). A survey of 115 African elephant females at AZA institutions found that dominant females were larger, more disciplinary, and more often reproductively acyclic (Freeman et al, 2004). The results from this study suggest the dominant female was Jo. She was involved in the most dominance interactions, was never submissive to another elephant, and was the only elephant to displace another individual. Over half of those displacements resulted in Jo eating or investigating an object previously used by the other female; usurping the resource of a herd mate may be akin to being less likely to share items, a trait associated with dominant females (Freeman et al, 2004). She is also the largest elephant and is reproductively acyclic, further supporting Freeman et al's (2004) survey.

Moshi and Tika were both submissive to Jo, the former to a larger degree. Submissive displays are used by subordinates to show that they will not retaliate against the dominant individual if challenged (Koontz & Roush, 1996). The subjects would lower their heads and turn around to back into the dominant's side, which is a typical display of submission in elephants that allows for physical contact while still protecting the more vulnerable head region (Estes, 1991; Garaï, 1992; Langbauer, 2000). In many ungulates subordinate individuals will also move away before a dominant individual comes into proximity, especially in stable relationships (e.g. Adams & Berg, 1980; Holand et al, 2004; Robitaille & Prescott, 1993); this occurred often, especially when Moshi was approached by Jo. Moshi and Jo rarely engaged in affiliative behavior, and Jo was seen head butting and mounting Moshi on several occasions (Mueller, pers. obs). Tika also displayed submissive behavior toward Jo but also engaged in more affiliative behavior with her and remained in social proximity; the two females were friends, a common relationship in group-living ungulates even when one individual is more dominant (Garaï, 1992; Mikulica, 1991). Tika was also friends with Moshi, based upon their levels of affiliation and proximity, but their hierarchical rank relative to each other was dependent upon their most dominant herd mate. Tika displayed submissive behavior toward Moshi and Moshi more often initiated affiliative interactions, which suggests that Moshi was the more dominant individual of this dyad. However, Tika was never submissive to Moshi in Jo's presence (Mueller, pers. obs.). Tika's friendship with Jo allowed Tika access to Jo's resources, including her dominance; Moshi was submissive toward Jo and therefore also submissive toward Tika when Jo was present. Relationships between the female were therefore based upon both dominance and affiliation; the hierarchy was not truly linear but relied upon the interactions of all group members together.

Abnormal behaviors were most often seen inside, primarily from Moshi and Jo. Both elephants usually ate while performing a stereotypic behavior, which has been described in other studies of captive elephants (e.g. Friend, 1999) and may suggest the behaviors are not in response to an immediate stressor. Concurrently performing a stereotypy and another behavior is common with well-established stereotypies that have become an automatic behavior pattern (Mason, 2006a). Also, animals experiencing high levels of acute stress often will cease eating (Clark et al, 1997). The abnormal behaviors seen in the elephants are therefore more likely due to habitual performance or low levels of chronic (long-term) stress rather than the presence of acute (short-term) stressors. Moshi displayed abnormal behaviors more often than any other individual and did not differ in her indoor performance in relation to social housing. She most often head bobbed, or rhythmically moved her head and shoulders up and down while shifting her weight between her front legs. Like Jo, she would often perform this stereotypy at a slow pace while engaging in other behaviors such as eating or investigation. The form of the behavior was invariant but the rate at which Moshi head bobbed did change; she would often head bob at a much faster rate in social situations, such as when other elephants were vocalizing or when another elephant was within view and engaged in solitary aggression. The most intense occurrences were seen when the shift door between the two indoor enclosures was open, giving all three elephants access to the entire indoor exhibit; during these times Moshi was in forced proximity to Jo, with whom she was highly submissive (Mueller, pers. obs.). When housed outside Moshi would sometimes head bob when approached by Jo or when displaying a submissive posture. Given the prevalence of this behavior it is likely often performed out of habit, but the heightened displays during potentially stressful situations indicate that it may have originated due to acute social stress and is still used as a coping response in similar circumstances.

Jo primarily swayed, which is a common behavior seen in both zoo and circus housed elephants. When Jo was housed inside she displayed abnormal behavior significantly less when housed alone than with Tika, instead increasing locomotion and object investigation. Jo would sometimes walk at a fast pace and repeatedly investigate the door separating her and Tika; her inability to reach Tika may have been an acute stressor (Carlstead, 1996). When with Tika she would sway at a slow pace, typically while eating. Female elephants in the wild and in captivity are known to form special relationships, or friendships, with herd mates (Garaï, 1992). Females bonds have been associated with lower stress hormone concentrations in rodents (Sachser et al, 1998), and involuntary separation of bonded animals can cause an immediate increase in stress hormones (Mendoza et al, 2000). Although Jo showed low amounts of social behavior when housed inside with Tika, having Tika in proximity to her may have been comforting. It is thought that, even in social species, time spent in proximity is probably a more accurate determination of bonded female relationships than social interaction (Garaï, 1992; Wilson et al, 2006). The swaying may therefore have been performed as a habit instead of a coping response, seen in a non-stressful situation simply because it has become a part of Jo's behavioral repertoire. It is also possible that the swaying was a response to the chronic stress of the enclosure but that when housed alone the acute social stress elicited a different and more intense response that superceded her response to the chronic environmental stress (Bashaw et al, 2001; Mason, 1991)

Rhinos: Rhinos showed differences in social behavior based upon sex and age when housed inside. The females displayed more agonistic behavior, which may have been a factor of their closer social proximity. Although all individuals could interact with each other through the bars of the indoor enclosure, the male was the only individual with full control over social proximity. The male could choose whether or not to be proximate to or interact with another individual, whereas the choice of each female was affected by the choice of the other female. This social housing increases the likelihood rhinos will interact and/or compete for space or resources. The increased affiliative and sexual behavior seen in the adults as compared to the juvenile was likely the result of reproductive state. In the wild adult male and female rhinos are solitary and generally interact with each other only for reproductive purposes (Schenkel & Schenkel-Hulliger, 1969). Captive rhinos likely show similar behavioral patterns, preferring to interact with other adults most often for sexual purposes.

The female rhinos were seen engaging in agonistic encounters, but these were rare and not associated with any known independent variable or managerial factor. Aggression between females in one captive herd of white rhinos was also rare and the authors suggested it was likely biologically insignificant (Swaisgood et al, 2006). Given that the Kibibbi was nearing maturity and Inge was pregnant these behaviors may have been a factor of natural behavior –when a female is nearing parturition in the wild her older calf will disperse, often encouraged with increased aggression from the mother (Schenkel & Schenkel-Hulliger, 1969). In captivity, however, a female does not always have the choice as to when a juvenile is separated, and this may have been motivation for the agonistic behavior between Inge and Kibibbi. In wild habitats with stable populations and ample resources a previously separated subadult female may rejoin its dam and sibling, and if another calf is not born a female may not disperse at all (Schenkel & Schenkel-Hulliger, 1969). Schenkel & Schenkel-Hulliger (1969) saw a stable group of three black rhinos that were thought to be a dam and her adult and subadult offspring. Female black rhinos can likely maintain affiliative social relationships even with subadult and adult female offspring. Captive rhinos are generally kept with their dams until puberty (Hutchins & Kreger, 2006), but females can may remain with dams indefinitely provided the enclosure provides ample space and aggression rates between individuals remain low.

Female white rhinos, either captive or wild, do not form true dominance hierarchies (Mikulica, 1991; Swaisgood et al, 206), but Carlstead et al (1999a) found that in black rhinos older females tended to have more dominant qualities. Inge, the mother, was expected to be dominant over Kibibbi, the subadult daughter, as is typical of ungulates (e.g. van Dierendonck et al, 1995). Both rhinos were seen displacing each other, as opposed to only the dominant individual displacing others within the elephant group. The pattern seen in the rhinos has also been seen in feral horses, a closely related species (Heitor et al, 2006a). When housed inside Inge performed the only displacements and did not initiate any affiliative behavior toward Kibibbi. With fewer resources and less space in that enclosure it was expected that the more dominant animal would exert more control over its space and behaviors, as Inge did by claiming resting spots and avoiding most social activity. Kibibbi did displace Inge outside but with more abundant space and resources even the more dominant individual might not have needed to control any particular area, and may have chosen to leave the subordinate individual rather than initiate an aggressive interaction. Inge left Kibibbi more often than she approached her in both enclosures, which further supports her dominance and more solitary nature.

Among the rhinos, Jimma displayed the most abnormal behavior, primarily pacing. Jimma displayed less pacing in the back yard as compared to both the front yard and inside enclosure and also rested significantly more in the back yard. High levels of resting are often equated with boredom or a lack of behavioral opportunities in captive animals (Carlstead, 1996; Frézard & LePape, 2003), but species with naturally high levels of inactivity should be expected to spend large amounts of time resting. Frézard & LePape (2003) found that wolves housed in larger enclosures spent more time resting, which was unexpected due to the increased space and opportunity for movement; the authors suggested that the enclosures provided the animals with more spatial control, allowing them a choice as to where to rest and thus decreasing stress. It is possible that the back yard, although smaller and less environmentally diverse than the front yard, resulted in Jimma decreasing abnormal behaviors and increasing resting behavior because of its lack of human disturbances. Surveys of multiple zoos housing black rhinos found that the percent of the outdoor enclosure with public access was positively correlated with mean levels of glucocorticoids, mortality, and fearful behavior, while the size of the enclosure was not (Carlstead & Brown, 2005; Carlstead et al, 1999b). Human presence may therefore have a greater impact on stress in this species than available space. Zoo visitors are an unpredictable variable and can often be perceived as a threat, especially in species such as black rhinos that are naturally wary of humans (Morgan & Tromborg, 2007; Schenkel & Schenkel-Hulliger, 1969); even after long periods in captivity this aversive reaction can affect behavior (Carlstead & Brown, 2005). The front yard is the only rhino enclosure at CMZ with public access and this may have negatively influenced Jimma's performance of abnormal behaviors. Keeping species such as the black rhino visible while still allowing the animals the ability to control their exposure to humans is challenging (Morgan & Tromborg, 2007). At CMZ zoo visitors had access to approximately 17.22% of the front yard perimeter; while this number is relatively low and the visitor platforms were above eye level of the rhinos, the platforms were directly adjacent to the exhibit. Rhinos may benefit from enclosures that have not only decreased public access but also greater distance between visitors and animals. Exhibit design in black rhinos is a critical variable in animal welfare and further work analyzing the effects of visitor presence is needed to determine proper management standards.

Other Abnormal Behaviors: Abnormal behaviors sometimes morphologically resemble natural behaviors. In these cases the performance is the primary factor, such as behaviors seen during inappropriate circumstances, using exaggerated displays, or at unnaturally high levels (Mason, 1991). This phenomenon was seen in both species, most often by the individuals who did not show high levels of more traditional stereotypies (i.e. Tika, Inge, and Kibibbi). These behaviors are difficult to interpret, as there is no precise definition as to when if ever these behaviors can be deemed abnormal (Mason, 1991). Mouthing, for example, resembles chewing behavior but is not associated with having food or other objects in the mouth; this was seen in both female rhinos. This oral stereotypy may be a response to lack of feeding opportunities, as foraging and chewing are essential and highly motivated behaviors in ungulates (Bergeron et al, 2006). A similar behavior of opening and closing the mouth has been described as a possible threat display in black rhinos (Schenkel & Schenkel-Hulliger, 1969), and Carlstead et al (1999a) suggested that mouthing in captivity may be associated with increased arousal or agitation either social or otherwise. Tongue-playing, which is typically considered an oral stereotypy in captivity, has been seen in wild giraffes after feeding; Veasey et al (1996) suggested it may not be abnormal but merely occurs at abnormally high levels in captivity. Mouthing has not been identified as a feeding-related behavior in wild rhinos but it is often difficult to identify at a distance and can often be mistaken for feeding; field studies specifically identifying mouthing would be needed to determine if and under what circumstances the behavior is seen. Recognizing possible origins for this behavior may help identify what captive variables may promote it and how it can be reduced.

One unexpected result was Tika's level of self-directed behavior; at almost two min/hr, it was nearly four times that of the other individuals. Generally this behavior consisted of Tika touching her face, head, and nipples. Self-directed behavior may be an effort to stimulate the nervous system (Carlstead, 1996). Lukas et al (2003) found that self-directed behavior in gorillas decreased when groups experienced environmental novelty via multiple enclosures and the behavior may thus be a response to lack of behavioral opportunities in the indoor enclosure. Tika also performed self-sucking behavior, using her trunk to suck on her nipples. Similar behaviors have been described in adults of other mammal species and are associated with premature maternal separation, suggesting that early weaning may have long-term behavioral effects (Mason, 2006b). Tika was brought into captivity when less than two years old; in the wild female African elephants are weaned gradually at three or four years of age and thereafter remain in their natal herd for life (Estes, 1991). Maternal separation may also lead to locomotor stereotypies, such as those shown by Jo and Moshi; they were also brought into captivity before two years of age. Early separation is well-documented to affect brain function and behavior in multiple species of primates and likely affects other mammal taxa as well (Bergeron et al, 2006; Mason, 2006b). The social system of African elephants is based upon related conspecifics and prematurely separating calves from their mothers may have consequences similar to those seen in primate species. Some animal managers believe that a lack of early social learning and subsequent lack of a true matriarch contribute to many of the behavioral problems seen in captive elephants (Olson & Wiese, 2000). Research relating maternal separation and early development in social species such as African elephants to later behavior problems is crucial in managing both captive and wild populations. Understanding the long-term effects of early rearing can potentially impact social housing, captive population management, and even translocation and culling in the wild.

Solitary aggression was seen in both species, including Tika, Inge, and Kibibbi; this behavior consisted of throwing and charging objects, aggressive displays, and vocalizing in a non-social context. Inge displayed solitary aggression most often, and the behavior is sometimes associated with increased agitations in black rhinos (Carlstead et al, 1999a). In Inge the behavior may have been due to environmental stress. The outdoor rhino enclosure was situated in front of both an access road and train tracks, and Inge's bouts of solitary aggression were often precipitated by the passing of large trucks or trains. Ambient noises, especially those that are loud, unnatural, and unpredictable, are a potential stressor to captive animals (Morgan & Tromborg, 2007). Savannah habitats have an extremely low level of ambient noise, averaging only 20-36 dB (Morgan & Tromborg, 2007), whereas truck and train traffic averages 80-100 dB (www.dangerousdecibels.org). Inge was imported from Africa when approximately four years old and may have difficulty coping with the loud and unpredictable noises often found in captive environments. The unnatural noises may also have been interpreted as a threat. Female black rhinos are sensitive to potential threats: they are more vigilant than males and once vigilant are more likely to charge (Berger & Cunningham, 1995). This behavior is enhanced in mothers (Berger & Cunningham, 1995), and during the study Inge was pregnant and housed with her juvenile daughter. Schenkel & Schenkel-Hulliger (1969) noted a behavior similar to solitary aggression, termed "redirected defensive aggression," in wild black rhinos: when individuals became tense due to human presence they would charge at animals such as antelopes or zebras because of their proximity and lack of threat. Inge's behavior may therefore also be due to the presence of zoo visitors, who could have been perceived as a potential threat similar to the loud ambient noises. Determining the specific causes of this behavior requires further work specifically linking occurrences to environmental variables, and the results would be valuable in assessing how to decrease environmental stress in black rhinos.

Summary and Conclusions

1. The elephants were not overtly aggressive and had a stable hierarchy. Tika was friends with both other elephants but Jo and Moshi showed little affiliative behavior. This can be potentially stressful to the subordinate animal (Carlstead, 1996; Morgan & Tromborg, 2007; Veasey, 2006) and zoo

managers should ensure that strictly dominant relationships among herd mates are not decreasing any individual's well-being.

2. Moshi and Jo's performance of abnormal behaviors was likely habitual but did show some variability. Acute social stress may have affected the performance of abnormal behaviors in these individuals, but further work is needed to clarify the relationship.
3. The female rhinos displayed more agonistic behavior than the elephants but aggression levels were still low. The aggression was likely due in part to Inge's reproductive state. Future studies should be done to examine how long females can be housed with their dams, and how this may relate to reproductive condition.
4. Jimma's increased level of pacing in the front outdoor enclosure may have been due to stress caused by exposure to zoo visitors. Future work relating abnormal behaviors in rhinos to enclosure design and public presence would be useful in clarifying any relationship between these variables.
5. Individuals of both species displayed abnormal behaviors that were morphologically similar to natural behaviors. Whether these behaviors can truly be deemed abnormal is not known, but their prevalence within these elephants and rhinos merits further investigation in a larger segment of the captive population.

Chapter 4: Behavioral Changes Associated with Disease in a Captive Black Rhinoceros

Introduction

The black rhinoceros (*Diceros bicornis*) is a critically endangered species with an estimated wild population of only 3600 individuals. Despite government regulations black rhinos continue to be illegally poached, and habitat loss due to human encroachment remains a constant threat (Hutchins & Kreger, 2006). Maintaining black rhinos in captivity is thus important to ensure the continuation of the species and provide a possible means of re-establishing the species in the wild. However, the captive black rhino population is not self-sustaining, and a primary contributor to this is the increased occurrence of disease in the captive population. Many of these diseases are of unknown origin and have not been described in the wild, making them difficult to effectively diagnose and treat (Dennis et al, 2007). Disease can not only affect the reproductive success and mortality of an individual but is also an indicator of decreased well-being (Clark et al, 1997). The ability to diagnose diseases earlier and provide quick and effective treatments could greatly improve the management of captive black rhinos.

Diseases in zoo animals can be challenging to diagnose: they are often of unknown origin; diagnostic tests may not be evaluated for the particular species; and physical examinations can be difficult for veterinarians to perform, especially with larger animals such as rhinos (Dennis et al, 2007; Hutchins &

Kreger, 2006). Zoo animal caretakers must therefore rely upon outward symptoms to assist in disease detection and treatment. Changes in normal behavioral patterns are often the first indication of illness in animals and can provide useful information related to an individual's overall health and well-being without invasive procedures (Clark et al, 1997). Behavior is often analyzed in conjunction with disease occurrence in livestock to provide information for more efficient diagnoses (e.g. Corke & Broom, 1999; Galindo & Broom, 2002; Healy et al, 2002); a better understanding of behavior and disease in zoo animals would allow for similar practices

During the course of a behavioral study, a four-year-old female black rhino housed at Cleveland Metroparks Zoo was diagnosed with a staphylococcus infection in March 2007 after displaying physiological signs of illness. The objective of this study was to analyze how behavior changed in relation to the onset and progression of the illness, and how behavior differed overall between pre- and post-diagnostic months. The results suggest that identifying patterns related to both active and inactive behaviors can be useful in evaluating the health of black rhinos and should be implemented as a supplement to veterinary procedures.

Methods and Materials

Subject

Subject was a four-year-old female eastern black rhinoceroses (*D.b.* michaeli) housed at Cleveland Metroparks Zoo. Kibibbi was born at CMZ in 2003 and housed socially with her dam. CMZ also held an unrelated male black rhino, housed within proximity to but physically separated from the two females. Neither adult rhino showed signs of illness over the course of the study. Rhinos were handled under a protected contact system which included daily training sessions and daily or semi-daily presentation of enrichment. Hay and fresh water were available throughout the day.

Housing

The subject was housed in an exhibit consisting of indoor and outdoor enclosures. The <u>indoor enclosure</u> contained five adjacent stalls (each 29.77 m^2) with concrete substrates. When housed inside the rhinos were given access to more than one stall with the male separated from the females. The stall walls consisted of four horizontal metal bars that allowed for visual, oftactory, auditory, and some tactile contact between separated individuals. The ceiling contained multiple skylights and artificial lighting was only used when needed by the keepers. Zoo visitors could not enter the rhino barn but instead utilized a large viewing window at the front of the barn above the animals' level. The <u>front outdoor enclosure</u> was approximately 2160 m^2 and consisted of both level and sloped areas composed of various substrates, and included a pool, mud wallow, and multiple logs and wooden scratching posts. Two viewing platforms were available for zoo visitors, both directly above the animals' level; the remaining perimeter consisted of either tall vertical wooden plank fencing, rock walls, or short post fencing with a top rail and bottom wire backed by thick shrubs. Subject was primarily observed in the indoor enclosures only during inclement weather and/or low temperatures. When housed inside and ambient temperatures allowed, the doors of the enclosure remained open to allow for air circulation. When temperatures dropped below approximately 10°C the enclosure doors were closed and the building maintained at 18-21°C.

Data Collection and Analysis

Data were collected using 20-minute continuous focal animal observations (Lehner, 1996). Continuous sampling provides the most complete record of behavior and allows for frequency, rate, and bout lengths to be accurately calculated (Crocket, 1996). The ethogram was exhaustive and mutually exclusive (see Appendix 2). Data were recorded on the HP® iPAQ pocket PC h2215 using Pocket Observer® 2.0 software (Noldus Information Technology, Inc, Wageningen, The Netherlands). The subject was observed once per day, three days per week between 9:00 AM and 5:00 PM. Observations were balanced between AM (900-1259) and PM (1300-1700) hours. Data were collected from June 2006 through July 2007 for a total of 52 hours. Data were summarized using

Noldus Observer® 5.0 (Noldus Information Technology, Inc, Wageningen, The Netherlands) and Microsoft® Excel XP software (Microsoft Corporation, Redmond, WA). Due to the small sample sizes pseudoreplication was used and results are thus presented using descriptive statistics with significance determined based on overlap of respective standard errors of the mean (Crockett, 1996; Kuhar, 2006). Activity budget was calculated by averaging the weekly time (min/hr) spent exhibiting each behavior and averaging those values for a monthly mean. Data include both inside and outside observations unless otherwise specified. All results are presented as mean±SEM.

Results

Prior to exhibiting outward signs of illness Kibibbi's average time spent resting was 23.49±1.91 min/hr (June '06-Feb '07); during the month of March she averaged 53.21±2.7 min/hr, a significant increase from previous levels.

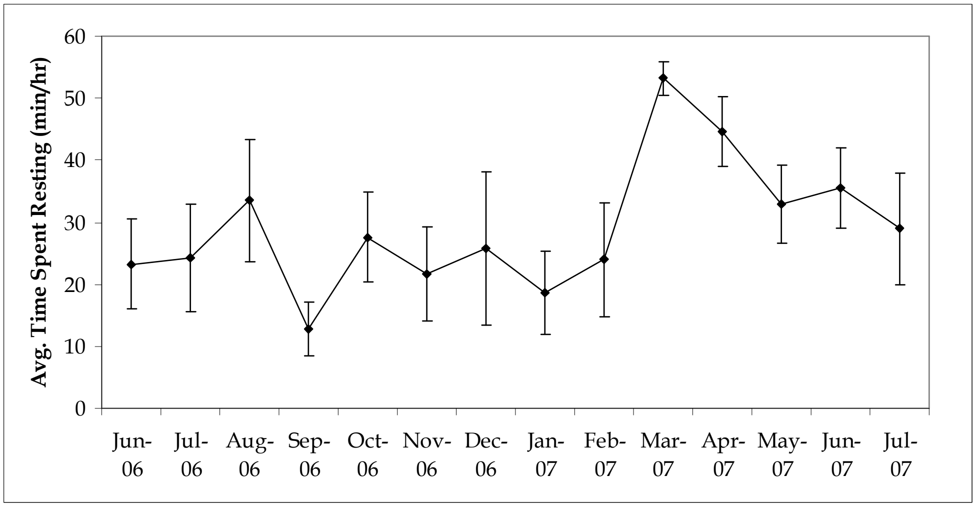


Figure 1. Monthly trends in mean resting behavior. Subject significantly increased resting in March 2007, the month she was diagnosed with a bacterial infection. Resting decreased each following month during the course of veterinary treatment and the behavior returned to pre-diagnosis levels by July.

Beginning in October 2006 Kibibbi showed a steady decline in amount of time locomoting, and in December object investigation also decreased. Both behaviors reached a low in March 2007 and thereafter began to increase.

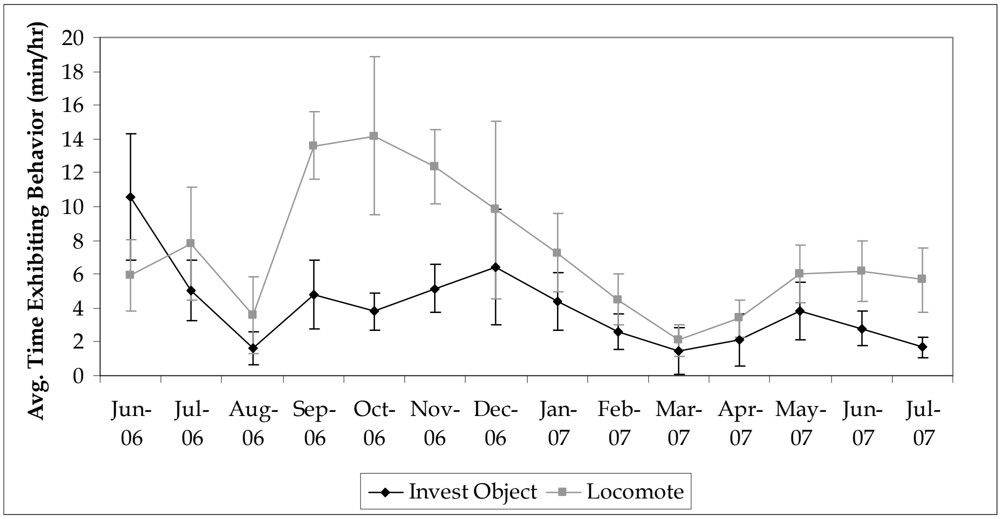


Figure 2. Monthly trends in mean investigatory and locomotory behavior. Subject began decreasing locomotion in October and investigation in December of 2006. Both behaviors were lowest during March 2007 and began increasing the following month.

To account for possible effects of increased time spent in the indoor enclosure, comparisons of inside observations directly before (Dec 2006-Feb 2007) and after (March – May 2007) the diagnosis were conducted. Kibibbi significantly decreased eating, locomotion, and enrichment investigation. The only behavior to increase between these periods was resting (22.22±5.94 [pre] vs. 44.11±4.66 [post] min/hr)

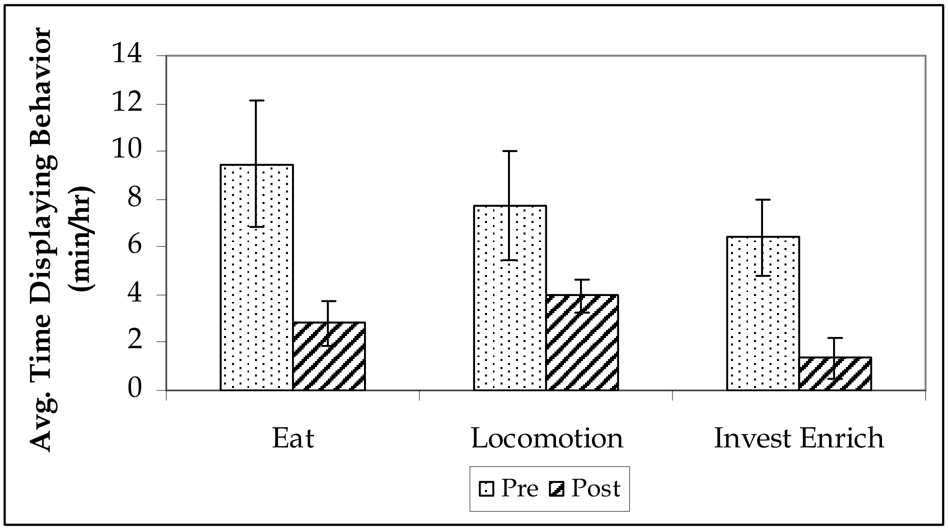


Figure 3. Comparisons of active behaviors pre- and post-diagnosis. Data include only time in the indoor enclosure to control for housing effects. Subject decreased time spent eating, locomoting, and using enrichment after diagnosis.

Kibibbi also performed fewer urine sprays during the months surrounding the diagnosis. Her average rate from June 2006 – January 2007 was 2.17±0.20/hr; her average rate from February – June 2007 was 0.14±0.04/hr. No urine sprays were seen in March 2007.

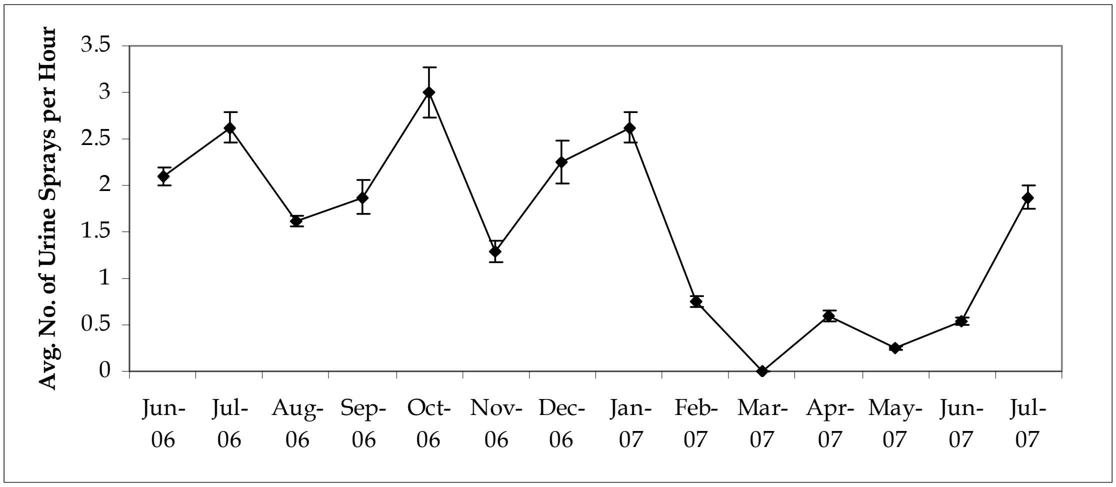


Figure 4. Monthly trends in mean rate of urine spraying. Subject decreased urine spraying beginning in February 2007, one month prior to diagnosis; no urine sprays were seen in March. Mean rates began to rise in April and returned to pre-diagnosis levels by July.

Discussion

Behavior is often a primary indicator of illness and therefore is important in regards to captive animal health, yet little scientific evidence is available directly linking changes in behavior with disease (Clark et al, 1997; Hutchins & Kreger, 2006). Intuition and experience are often used to link behavior and health in domestic and livestock animals (Broom, 2006; Clark et al, 1997), but the natural behavior and biology of exotic species housed in zoos are often not as well understood as those of domesticated species. For species such as the black rhino that have high rates of disease a better understanding of how behavior directly relates to illness could improve diagnoses and treatments in zoos.

Both long-term and short-term immune responses require energy, and as a result many behavioral changes due to disease act to conserve energy (Broom, 2006). During the month of diagnosis Kibibbi significantly increased time spent resting. Exhaustion and inactivity are often associated with illness in animals (Broom, 2006; Clark et al, 1997; Corke & Broom, 1999; Hutchins & Kreger, 2006). Resting assists in recovery from disease by conserving energy for use by the immune system, and may also be a response to pain or discomfort (Broom, 2006). Sudden and significant changes in resting behavior in black rhinos may therefore indicate illness and should be immediately investigated. Unlike resting behavior, changes in active behaviors were seen before the physiological signs of disease were apparent. Excessive activity during the acute phase of an illness can decrease the body's disease-fighting ability by diverting energy away from the immune system (Broom, 2006). Behaviors such as locomotion and object investigation are not immediate biological requirements, especially in a captive environment where finding food or escaping potential threats is not a concern. These types of behaviors may thus be the first that are reduced when increased energy is required of the immune system, and changes in these behavioral patterns may be an early indicator of disease.

Increased time indoors may have also affected time spent locomoting and investigating objects, but when enclosure type was controlled for Kibibbi still had overall lower levels of eating, locomoting, and investigation during the illness. Changes in diet are often among the first signs of illness in the black rhino (Hutchins & Kreger, 2006) and changes in diet and excretory behavior have been described with other diseases in this species (e.g. Neiffer et al, 2001). Appetite loss is one effect of the acute-phase response of the immune system and in the short-term is not immediately harmful. Cessation of eating decreases digestion and therefore allows energy and blood defenses to be diverted to the immune system, or may be the effect of pain or discomfort (Broom, 2006; Gregory, 1998). Prolonged anorexia, however, can be detrimental to the overall immune response and can indicate that a disease is worsening or treatment is ineffective (Broom, 2006). Any dietary changes in black rhinos should be immediately addressed and continuously monitored over the course of treatment.

Urine spraying is a species-typical behavior of black rhinos that is thought used for social communication. Black rhinos are not territorial and generally share home ranges with many conspecifics; urine spraying can communicate an individual's location and movement patterns without direct social contact, which is important for solitary animals (Schenkel & Schenkel-Hulliger, 1969). Kibibbi began to decrease the rate of urine spraying one month prior to diagnosis, which could be due to a number of factors. Animals will often avoid conspecifics when ill, which is thought in part to prevent disease transmission (Broom, 2006; Gregory, 1998); although black rhinos are not highly social the decrease in urine spraying may be the result of this adaptive behavior. The decrease could also be similar to that of the other active behaviors, with energy beginning to divert to more immediate needs during the first stages of illness. Although this behavior was more infrequent than other active behaviors the large change in performance suggests it could also be used as an indicator of disease onset in this species.

Research focusing on the behavior of both healthy and diseased rhinos would provide more comprehensive information on normal versus abnormal behavior (Healy et al, 2002) that could then be applied by zoo employees as a means of preliminary evaluation. Behavior alone cannot be used as proof of health status, but when combined with other measures it can provide useful information to zoo managers and veterinarians. Increased knowledge of black rhinoceros behavior and disease is vital in improving standards for captive husbandry and management (Dennis et al, 2007; Hutchins & Kreger, 2006), and the ability to detect disease earlier via behavioral observations could potentially increase the effectiveness of veterinary treatment and help save this critically endangered species.

Conclusion

Behavior is a primary method for zoo staff and visitors to evaluate an animal's welfare (Carlstead, 1996). Displaying behaviors seen in the wild is ideal and desirable for zoo-housed animals, but lacking the behavioral diversity and exact activity budgets does not necessarily imply a lack of good welfare (Frézard & LePape, 2003; Veasey et al, 1996). Animal species do not have one specific behavior pattern, especially adaptable species such as elephants and rhinos, which in the wild are widely distributed in variable habitats (Hutchins, 2006). The behavior of wild animals is affected by multiple environmental and social variables and hence different populations of a species will exhibit different behavioral activity budgets (Carlstead, 1996; Hutchins, 2006; Veasey et al, 1996). Additionally, the behavior of wild animals can be difficult to accurately record, and the methods used to do so can make comparisons to other studies problematic (Veasey et al, 1996). The goal of zoos should therefore be activity budgets comprised of natural solitary and social behaviors with minimal abnormal behaviors, aggression, and lethargy; behavior of wild individuals should be used as a guideline and not a stringent goal (Hutchins, 2006).

The main difference between wild and captive environments is the degree of control (Carlstead, 1996). Captive environments present many of the same potential stressors as are seen in the wild, such as visual, audio, and olfactory cues, or changes in temperatures or substrates (Morgan & Tromborg, 2007). In the wild, however, individuals are able to better control their exposure to these variables. Captive elephants and rhinos should be housed in enclosures that provide both space and behavioral options; they should be able to perform species-typical behaviors, have access to physical resources such as environmental objects and enrichment, and be able to control their proximity to both conspecifics and zoo visitors. Providing environments and husbandry practices that satisfy the behavioral needs of elephants and rhinos is necessary to ensure the well-being of these species.

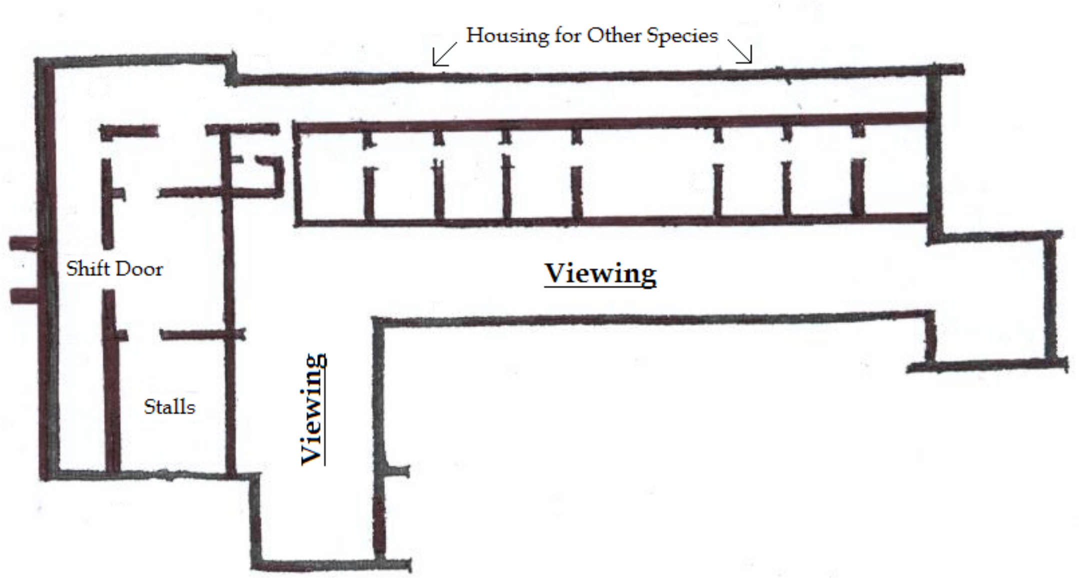
Housing African mammals in northern climates provides additional challenges for zoos, but with proper housing and management individuals can likely adapt to increased time spent indoors. Animals should be given outdoor access as much as possible without compromising health or safety (Hutchins & Kreger, 2006), and indoor enclosures should encourage species-typical behaviors. Elephants and rhinos need indoor enclosures that can accommodate their behavioral and physical needs just as outdoor enclosures do, with space for locomotion, opportunities for activity, and appropriate substrates (Hutchins, 2006). Zoos can use enrichment items or changes in enclosure composition to provide novelty and stimulate activity. Even in northern climates animals should be given outdoor access as much as possible without compromising health or safety (Hutchins & Kreger, 2006).

Proper social housing is a welfare concern in both African elephants and black rhinos, as social instability is well documented to be stressful to animals (Morgan & Tromborg, 2007). Low levels of aggression and stable herd relationships are associated with greater reproductive success in horses, with increased aggression resulting in decreased conception and increased fetal and foal mortality (Linklater, 2000). For species with low levels of reproduction such as elephants and rhinos, ensuring captive groups are not experiencing social stress is imperative. Both species have been successfully housed in captivity in unnatural social groups, suggesting that individual compatibility is probably more important than whether group compositions are similar to those seen in the wild (Hutchins, 2006). Zoos should strive to evaluate social groups to determine levels of aggression and affiliation among all individuals and whether group composition is impacting the welfare of any animal. Further research on social behavior in relation to group composition, breeding, and calf rearing is needed to improve management and increase the reproductive success of elephants and rhinos (Olson & Wiese, 2000; Vidya & Sukumar, 2005).

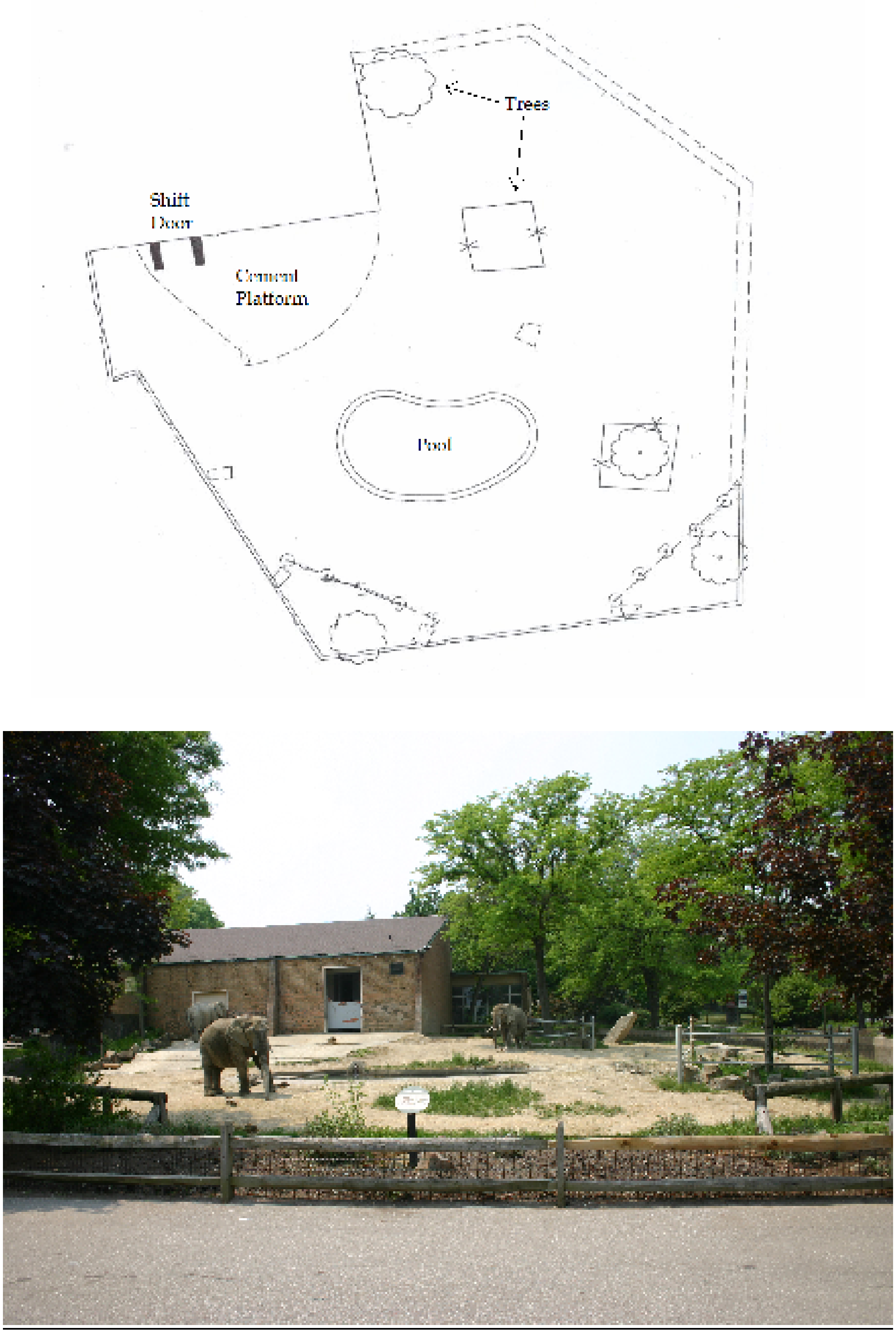
Abnormal behaviors are also a concern in African elephants and black rhinos; these behaviors are considered more prevalent in ungulates than in other mammal taxa (Bergeron et al, 2006). Abnormal behaviors have been suggested to be beneficial when used as a coping response to prevent an individual from entering a depressed state, but no definitive evidence for this claim exists (Mason, 1991; Mason, 2006a). Even if the behavior is beneficial in the immediate situation, the need for a coping response suggests an unnatural interaction between the animal and its environment (Mason, 1991). The occurrence of an abnormal behavior in captivity should thus always be examined to determine the possible motivations behind it and how the environment can be improved to lessen those motivations. Despite the idiosyncratic nature of these behaviors, studies such as this utilizing small sample sizes can help to uncover any species-wide patterns in motivation, performance, or successful reduction. Additional research examining the performance of abnormal behaviors and the effects of various environmental and social enrichment techniques would help to further understand how these behaviors can be reduced in captivity.

Captive African elephants and black rhinos have numerous population-wide behavioral and health concerns which may be due in part to an inability to cope with their physical and social environments (Brown et al, 2001). The purpose of behavioral research in zoos should be to determine whether the environments animals are experiencing encourage the best possible welfare. Studies such as this that focus on behavior, sociality, and exhibit use and preferences are necessary to improve the management and husbandry practices of these species and ensure they can be properly housed in captivity.

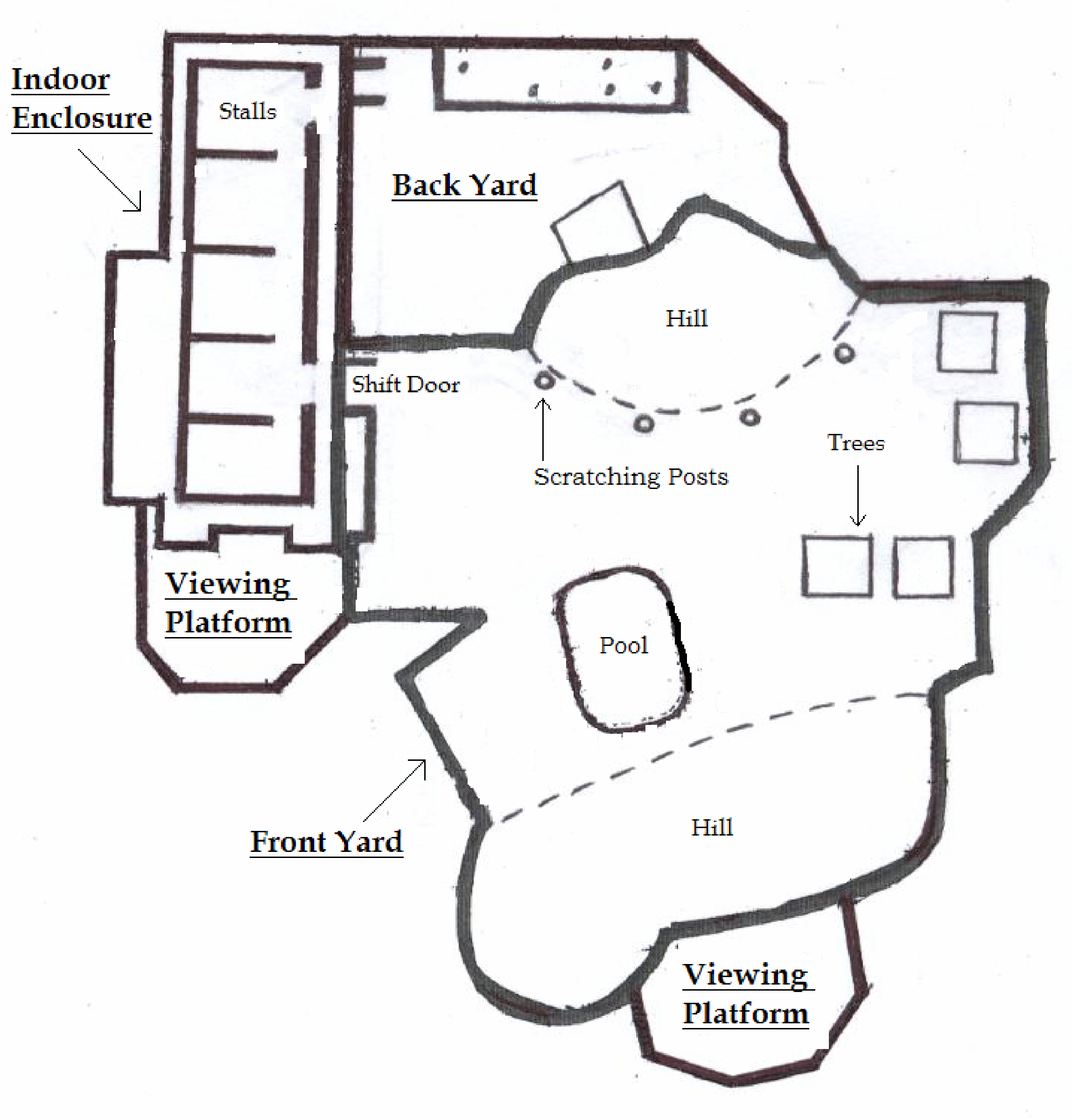
Appendix 1: African Elephant and Black Rhinoceros Enclosures at Cleveland Metroparks Zoo



Indoor African Elephant Enclosure



Outdoor African Elephant Enclosure



Indoor and Outdoor Black Rhinoceros Enclosures

Indoor Black Rhinoceros Enclosure

Outdoor Front Black Rhinoceros Enclosure

Appendix 2: Ethograms

African Elephant Solitary Behaviors

Rest	Stationary with eyes open or closed and no other simultaneous behaviors; may include ear flapping; may be upright or lying on side
Drink	Ingestion of water
Eat	Ingestion of food
Elimination	urination and/or defecation
Locomotion	Movement in either a forward or backward direction at any speed
Self-Directed	Touching/rubbing/grooming own body with mouth, trunk or appendages; does not include self-suck
Object Rub	Rubbing body against any object or substrate; does not include object manipulation
Bathe/Wallow	Submerging all or part of body in water or mud and/or using trunk to toss water or mud onto body
Dust	Using trunk to too sand/dirt/dust onto body
Dig	Manipulating/moving substrate with foot or tusk
Investigate Object	Sniffing and/or manipulating environment (branches, rocks, etc); does not include enrichment items
Investigate Enrichment	Sniffing and /or manipulating enrichment items
Pace	Repeated locomotion across the same route for at least 10 seconds
Sway	Repeated shifting of weight from one foreleg to the other for at least five seconds
Head Bob	Repeated nodding of head up and down for at least five seconds; may include non-locomotive movement of feet/legs
Head Bang	Forcibly hitting front or side of head against object or substrate
Self-Suck	Using mouth or trunk to suck on specific area of own body
Solitary Aggression	Aggression aimed at environment, such as tusking, head butting, ripping up vegetation or throwing objects
Other Solitary	Any solitary behavior not listed
Not Visible	Individual and/or its behavior cannot be seen by the observer

African Elephant Social Behaviors

Greet	Ears held high and folded against body, trunk placed in conspecific's mouth
Caress	Rubbing trunk over body of conspecific
Trunk Tangle	Gently entwining trunks with conspecific; score focal subject as Mod1
Play	Energetic social affiliative behaviors such as sparring, trunk wrestling, chasing, and rolling; typically seen only in calves; score focal subject as Mod1
Threat	Ears wide, trunk forward, head raised; may include scraping the ground with forelegs, twitching the tail, or weaving
Charge: Mock	Ears wide and trunk raised while rushing toward conspecific; no contact is made
Charge: Serious	Ears wide, trunk held against body and tusks aimed at conspecific while rushing toward the individual; contact is made
Fight	Aggressive interaction that may include head butting, trunk wrestling, and tusk stabbing, often preceded by serious charge
Submission	Ears back, head lowered, back arched and trunk curled inward; individual may present rump and/or back into dominant conspecific
Approach	Individual moves to within proximity of conspecific
Leave	Individual moves out of proximity of conspecific
Displace	Individual approaches and overtakes position of conspecific
Other Social	Any social behavior not listed

Black Rhinoceros Solitary Behaviors

Rest	Stationary with eyes open or closed and no other simultaneous behaviors; may be upright or lying on side
Drink	Ingestion of water
Eat	Ingestion of food
Elimination	urination and/or defecation
Footscrape	Rapidly alternating hind feet across ground, typically associated with defecation
Urine Spray	Marking objects in environment with bursts of urine
Locomotion	Movement in either a forward or backward direction at any speed
Self-Directed	Touching/rubbing/grooming own body with mouth, or appendages
Object Rub	Rubbing body or horn against any object or substrate; does not include object manipulation
Bathe/Wallow	Submerging all or part of body in water or mud
Dig	Manipulating/moving substrate with foot or nose
Flehmen	Curling up underside of lip, typically with head raised
Investigate Object	Sniffing and/or manipulating environment (branches, rocks, etc); does not include enrichment items
Investigate Enrichment	Sniffing and /or manipulating enrichment items
Pace	Repetitive locomotion across the same route for at least 10 seconds
Sway	Repeated shifting of weight from one foreleg to the other for at least five seconds
Head Bang	Forcibly hitting front or side of head against object or substrate
Mouthing	Repetitive open-mouthed chewing motion not associated with eating for at least five seconds
Solitary Aggression	Aggression aimed at environment, such as ripping up vegetation or throwing objects
Other Solitary	Any solitary behavior not listed
Not Visible	Individual and/or its behavior cannot be seen by the observer

Black Rhinoceros Social Behaviors

Greet	Individual approaches and touches noses with conspecific
Affiliation	Gentle non-sexual social contact, including nudging heads or horns
Follow	Traveling behind or next to a conspecifics, within one body length
Anogenital Investigation	Individual sniffs anogenital region of conspecifics
Threat	Turning head from side to side or repeatedly jerking it upward; broadside displays; short, mincing charge-like steps
Charge: Mock	Head lowered, ears pricked, tail raised and upper lip curled while rushing toward conspecifics; no contact is made
Charge: Serious	Similar to mock charge but with contact; includes chasing
Fight	Aggressive interaction, such as horn butting, jousting or stabbing
Submission	Head low while backing away from dominant conspecifics
Sexual	Any courtship or copulatory behavior
Approach	Individual moves to within proximity of conspecific
Leave	Individual moves out of proximity of conspecific
Displace	Individual approaches and overtakes position of conspecific
Other Social	Any social behavior not listed

Social Proximity (African Elephant and Black Rhinoceros)

Contact/Proximate	Within one body length of or in contact with another individual
Distant	Greater than one body length from another individual, but still within view
Far Distant	Out of view of other individuals
Unknown	Proximity cannot be determined

Works Cited

Adams, J. & Berg, J.K. (1980). Behavior of African elephants (*Loxodonta africana*) in Captivity. Applied Animal Ethology 6: 257-276.

African Elephant Specialist Group (2004). *Loxodonta africana*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

African Rhino Specialist Group (2003a). *Ceratotherium simum*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

African Rhino Specialist Group (2003b). *Diceros bicornis*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

Altmann, J (1974). Observational Study of Behavior: Sampling Methods. Behaviour 48: 227-265.

Archie, E.A., Morrison, T.A., Foley, C.A.H., Moss, C.J., Alberts, S.C. (2006). Dominance Rank Relationships Among Wild Female African Elephants, *Loxodonta africana*. Animal Behaviour 71: 117-127.

Asian Elephant Specialist Group (1996). *Elephas maximus*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

Asian Rhino Specialist Group (1996a). *Dicerorhinus sumatrensis*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

Asian Rhino Specialist Group (1996b). *Rhinoceros sondaicus*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

Asian Rhino Specialist Group (1996c). *Rhinoceros unicornis*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. www.iucnredlist.org. Downloaded on 15 October 2007.

Bashaw, M.J., Tarou, L.R., Maki, T.S., Maple, T.L. (2001). A Survey Assessment of Variables Related to Stereotypy in Captive Giraffe and Okapi. Applied Animal Behaviour Science 73: 235-247.

Benyus, J..M. (1992). Beastly Behaviors. Addison-Wesley Publishing Company: Reading, Massachusetts.

Berger, J. & Cunningham, C. (1995). Predation, Sensitivity, and Sex: Why Female Black Rhinoceros Outlive Males. Behavioral Ecology 6: 57-64.

Berger, J. & Stevens, E.F. (1996). Mammalian Social Organization and Mating Systems. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 344-351.

Bergeron, R., Badnell-Waters, A.J., Lambton, S., Mason, G. (2006). Stereotypic Oral Behavior in Captive Ungulates: Foraging, Diet and Gastrointestinal Function. In: Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. G. Mason & J. Rushen (Eds.). CABI: Wallingford, United Kingdom, pp. 19-57.

Berkeley, E.V., Kirkpatrick, J.F., Schaffer, N.E., Bryant, W.M., Threlfall, W.R. (1997). Serum and Fecal Steroid Analysis of Ovulation, Pregnancy, and Parturition in the Black Rhinoceros (*Diceros bicornis*). Zoo Biology 16: 121-132.

Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I., Hart, J.A. (2007). African Elephant Status Report 2007: An Update from the African Elephant Database. Occasional Paper Series of the IUCN Species Survival Commission, No. 33. IUCN/SSC African Elephant Specialist Group. IUCN, Gland, Switzerland.

Brockett, R.C., Stoinski, T.S., Black, J., Markowitz, T., Maple, T.L. (1999). Nocturnal Behavior in a Group of Unchained Female African Elephants. Zoo Biology 18: 101-109.

Broom, D.M. (2006). Behaviour and Welfare in Relation to Pathology. Applied Animal Behaviour Science 97: 73-83.

Brown, J.L., Bellem, A.C., Fouraker, M., Wildt, D.E., Roth, T.L. (2001). Comparative Analysis of Gonadal and Adrenal Activity in the Black and White Rhinoceros in North America by Noninvasive Endocrine Monitoring. Zoo Biology 20: 463-486.

Brown, J.L., Walker, S.L., Moeller, T. (2004). Comparative Endocrinology of Cycling and Non-Cycling Asian (*Elephas maximus*) and African (*Loxodonta africana*) Elephants. General and Comparative Endocrinology 16: 360-370.

Buss, I.O. (1990). Elephant Life: Fifteen Years of High Population Density. Iowa State University Press: Ames, Iowa.

Carlstead, K. (1996). Effects of Captivity on the Behavior of Wild Mammals. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 317-333.

Carlstead, K. & Brown, J.L. (2005). Relationships Between Patterns of Fecal Corticoid Excretion and Behavior, Reproduction, and Environmental Factors in Captive Black (*Diceros bicornis*) and White (*Ceratotherium simum*) Rhinoceros. Zoo Biology 24: 215-232.

Carlstead, K., Brown,J.L., Seidensticker, J. (1993). Behavioral and Adrenocortical Responses to Environmental Changes in Leopard Cats (*Felis bengalensis*). Zoo Biology 12: 321-331.

Carlstead, K., Mellen, J.D., Kleiman, D.G. (1999a). Black Rhinoceros (*Diceros bicornis*) in U.S. Zoos: I. Individual Behavior Profiles and Their Relationship to Breeding Success. Zoo Biology 18: 17-34.

Carlstead, K., Fraser, J., Bennett, C., Kleiman, D.G. (1999b). Black Rhinoceros (*Diceros bicornis*) in U.S. Zoos: II. Behavior, Breeding Success, and Mortality in Relation to Housing Facilities. Zoo Biology 18: 35-52.

Chase, I.D., Tovey, C., Spangler-Martin, D., Manfredonia, M. (2002). Individual Differences versus Social Dynamics in the Formation of Animal Dominance Hierarchies. Proceedings of the National Academy of Science USA 99: 5744-5749.

Clark, J.D., Rager, D.R., Calpin, J.P. (1997). Animal Well-Being IV. Specific Assessment Criteria. Laboratory Animal Science 47: 586-597.

Corke, M.J. & Broom, D.M. (1999). The Behaviour of Sheep with Sheep Scab, *Psoroptes ovis* infestation. Veterinary Parasitology 83: 291-300.

Crocket, C.M. (1996). Data Collection in the Zoo Setting, Emphasizing Behavior. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 545-565.

Crooney, C.C. & Newberry, R.C. (2007). Group Size and Cognitive Processes. Applied Animal Behaviour Science 103: 215-228.

Dangerous Decibels. Dangerousdecibels.org. Downloaded on 22 April 2008.

Dantzer, R. (1986). Behavioral, Physiological and Functional Aspects of Stereotyped Behavior: A Review and a Re-Interpretation. Journal of Animal Science 62: 1776-1786.

Dennis, P.M., Funk, J.A., Rajala-Schultz, P.J., Blumer, E.S., Miller, R.E., Wittum, T.E., Saville, W.J.A. (2007). A review of some of the Health Issues of Captive Black Rhinoceroses (*Diceros bicornis*). Journal of Zoo and Wildlife Medicine 38: 509-517.

van Dierendonck, M.C., de Vries, H. Schilder, M.B.H (1995). An Analysis of Dominance, its Behavioral Parameters and Possible Determinants in a Herd of Icelandic Horses in Captivity. Netherlands Journal of Zoology 45: 362-385.

Douglas-Hamilton, I., Bhalla, S, Wittemyer, G., Vollrath, F. (2006). Behavioural Reactions of Elephants towards a Dying and Decreased Matriarch. Applied Animal Behaviour Science 100: 87-102.

Elzanowski, A. & Sergiel, A. (2006). Stereotypic Behavior of a Female Asiatic Elephant (*Elephas maximus*) in a Zoo. Journal of Applied Animal Welfare Science 9: 223-232.

Estes, R.D. (1991). The Behavior Guide to African Mammals. The University of California Press: Berkeley and Los Angeles.

Foley, C.A.H., Papageorge, S., Wasser, S.K. (2001). Noninvasive Stress and Reproductive Measures of Social and Ecological Pressures in Free-Ranging African Elephants. Conservation Biology 15: 1134-1142.

Foose, T.J. & Wiese, R.J. (2006). Population Management of Rhinoceros in Captivity. International Zoo Yearbook 40: 174-196.

Forthman, D.L. & Bakeman, R. (1992). Environmental and Social Influences on Enclosure Use and Activity Patterns of Captive Sloth Bears. Zoo Biology 11: 405-415.

Freeman, E.W., Weiss, E., Brown, J.L. (2004). Examination of the Interrelationships of Behavior, Dominance Status, and Ovarian Activity in Captive Asian and African Elephants. Zoo Biology 23: 431-448.

Frézard, A. & Le Pape, G. (2003). Contribution to the Welfare of Captive Wolves (*Canis lupus* lupus): A Behavioral Comparison of Six Wolf Packs. Zoo Biology 22: 33-44.

Friend, T.H. (1999). Behaviour of Picketed Circus Elephants. Applied Animal Behaviour Science 62: 73-88.

Friend, T.H. & Parker, M.L. (1999). The Effect of Penning Versus Picketing on Stereotypic Behaviour of Circus Elephants. Applied Animal Behaviour Science 64: 213-225.

Galindo, F. & Broom, D.M. (2002). The Effects of Lameness on Social and Individual Behavior of Dairy Cows. Journal of Applied Animal Welfare Science 5: 193-201.

Garai, M.E. (1992). Special Relationships Between Female Asian Elephants (*Elephas maximus*) in Zoological Gardens. Ethology 90: 187-205.

Garnier, J.N., Green, D.I., Pickard, A.R., Shaw, H.J., Holt, W.V. (1998). Non-invasive Monitoring of Pregnancy in Wild Black Rhinoceros (*Diceros bicornis* minor) by Faecal Steroid Analysis. Reproduction, Fertility, and Development 10: 451-458.

Garnier, J.N., Holt, W.V., Watson, P.F. (2002). Non-invasive Assessment of Oestrous Cycles and Evaluation of Reproductive Seasonality in the Female Wild Black Rhinoceros (*Diceros bicornis* minor). Reproduction 123: 877-889.

Gregory, N.G. (1998). Physiological Mechanisms Causing Sickness Behaviour and Suffering in Diseased Animals. Animal Welfare 7: 293-305.

Gruber, T.M., Friend, T.H., Gardner, J.M, Packard, J.M., Beaver, B., Bushong, D. (2000). Variation in Stereotypic Behavior Related to Restraint in Circus Elephants. Zoo Biology 19: 209-221.

Healy, A.M., Hanlon, A.J., Weavers, E., Collins, J.D., Doherty, M.L. (2002). A Behavioural Study of Scrapie-Affected Sheep. Applied Animal Behaviour Science 79: 89-102.

Heitor, F., do Mar Oom, M., Vicente, L. (2006a). Social Relationships in a Herd of Sorraia Horses Part I. Correlates of Social Dominance and Contexts of Aggression. Behavioural Processes 73: 170-177.

Heitor, F., Mar Oom, M., Vicente, L. (2006b). Social Relationships in a Herd of Sorraia Horses Part II. Factors Affecting Affiliative Relaitionships and Sexual Behaviors. Behavioural Processes 73: 231-239.

Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M.E., Røed, K.H., Nieminen, M., Weladji, R.B. (2004). Social Rank in Female Reindeer (*Rangifer tarandus*): Effects of Body Mass, Antler Size and Age. Journal of Zoology London 263: 365-372.

Hutchins, M (2006). Variation in Nature: Its Implications for Zoo Elephant Management. Zoo Biology 25: 161-171.

Hutchins, M. & Kreger, M.D. (2006). Rhinoceros Behaviour: Implications for Captive Management and Conservation. International Zoo Yearbook 40: 150-173.

International Rhino Foundation. www.rhinos-irf.org. Downloaded on 15 October 2007.

International Species Information System. www.isis.org. Downloaded on 15 October 2007.

Kiwia, H.Y.D. (1986). Diurnal Activity Pattern of the Black Rhinoceros (*Diceros bicornis* L.) in Ngorongoro Crater, Tanzania. African Journal of Ecology 24: 89-96.

Koontz, F.W. & Roush, R.S. (1996). Communication and Social Behavior. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 334-343.

Kretzschmar, P., Ganslosser, U., Goldschmid, A., Aberham, A. (2002). Stimulation of Territorial and Mating Behaviour by Faecal Samples: A Comparative Study on Behaviour of Captive and Free-Living White Rhinoceros. In: A Research Update on Elephants and Rhinos – Proceedings of the International Elephant and Rhino Research Symposium, Vienna, June 7-11, 2001. H.M. Schwammer, T.J. Foose, M. Fouraker, D. Olson (Eds.). Schüling: Münster, pp. 299-302.

Kuhar, C.W. (2006). In the Deep End: Pooling Data and Other Statistical Challenges of Zoo and Aquarium Research. Zoo Biology 25: 339-352.

Lane, J. (2006). Can non-invasive Glucocorticoid Measures Be Used Reliable Indicators of Stress in Animals? Animal Welfare 15: 331-342.

Langbauer, Jr., W.R. (2000). Elephant Communication. Zoo Biology 19: 425-445.

Lehner, P.N. (1996). Handbook of Ethological Methods, Second Edition. Cambridge University Press: Cambridge, United Kingdom.

Lemonick, M.D. (2006). Who Belongs in the Zoo? Time 19 June 2006: 50-52.

Linklater, W.L. (2000). Adaptive Explanation in Socio-Ecology: Lessons from the Equidae. Biological Reviews 75: 1-20.

Lukas, K.E., Hoff, M.P., Maple, T.L. (2003). Gorilla Behaviour in Response to Systematic Alteration between Zoo Enclosures. Applied Animal Behaviour Science 81: 367-386.

Mallapur, A., Qureshi, Q., Chellam, R. (2002). Enclosure Design and Space Utilization by Indian Leopards (*Panthera pardus*) in Four Zoos in Southern India. Journal of Applied Animal Welfare Science 5: 111-124.

Maple, T.L. & Perkins, L.A. (1996). Enclosure Furnishings and Structural Environmental Enrichment. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 212-222.

Mason, G.J. (1991). Stereotypies: A Critical Review. Animal Behaviour 41: 1015-1037.

Mason, G. (2006a). Stereotypic Behaviour in Captive Animals: Fundamentals and Implications for Welfare and Beyond. In: Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. G. Mason & J. Rushen (Eds.). CABI: Wallingford, United Kingdom, pp. 325-356.

Mason, G. (2006b). Maternal Deprivation and Stereotypy in Animals other than Primates. In: Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. G. Mason & J. Rushen (Eds.). CABI: Wallingford, United Kingdom, p. 170.

Mason, G.J. & Latham, N.R. (2004). Can't Stop, Won't Stop: Is Stereotypy a Reliable Animal Welfare Indicator? Animal Welfare 13: 557-569.

Mason, G. & Mendl, M. (1993). Why is There No Simple Way of Measuring Animal Welfare? Animal Welfare 2: 301-319.

Mason, G.J., Clubb, R., Latham, N., Vickery, S. (2007). Why and How Should We Use Environmental Enrichment to Tackle Stereotypic Behaviour? Applied Animal Behaviour Science 102: 163-188.

McComb, K., Moss, C., Sayialel, S., Baker, L. (2000). Unusually Extensive Network of Vocal Recognition in African Elephants. Animal Behaviour 59: 1103-1109.

Mech, L.D. (1970). The Wolf: The Ecology and Behavior of an Endangered Species. University of Minnesota Press: Minneapolis.

Mench, J.A. & Kreger, M.D. (1996). Ethical and Welfare Issues Associated with Keeping Wild Mammals in Captivity. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 5-15.

Mendoza, S.P., Capitanio, J.P., Mason, W.A. (2000). Chronic Social Stress: Studies in Non-human Primates. In: The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare. G.P. Moberg & J.A. Mench (Eds). CABI Publishing: New York, pp. 227-247.

Mikulika, V. (1991). Social Behaviour in Two Captive Groups of White Rhinoceros (*Ceratotherium simum simum* and *Ceratotherium simum cottoni*). Der Zoologische Garten 61: 365-385.

Mills, L.J. (1997). Behavioural Characteristics Used to Determine Reproductive Status of Captive Black Rhinoceroses (Diceros bicornis michaeli). Der Zoologische Garten 67: 271-278.

Morimura, N. & Ueno, Y. (1999). Influences on the Feeding Behavior of Three Mammals in the Maruyama Zoo: Bears, Elephants, and Chimpanzees. Journal of Applied Animal Welfare Science 2: 169-186.

Neiffer, D.L., Klein, E.C., Wallace-Switalski, C. (2001). *Leptospira* Infection in Two Black Rhinoceroses (*Diceros bicornis michaeli*). Journal of Zoo and wildlife Medicine 32: 476-486.

Ntumi, C.P., van Aarde, R.J., Fairall, N., de Boer, W.F. (2005). Use of Space and Habitat by Elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. South African Journal of Wildlife Research 35: 139-146.

Olson, D. & Wiese, R.J. (2000). State of the North American African Elephant Population and Projections for the Future. Zoo Biology 19: 311-320.

Patton, M.L., Swaisgood, R.R., Czekala, N.M., White, A.M., Fetter, G.A., Montagne, J.P., Rieches, R.G., Lance, V.A. (1999). Reproductive Cycle Length and Pregnancy in the Southern White Rhinoceros (*Ceratotherium simum* simum) as Determined by Fecal Pregnane Analysis and Observations of Mating Behavior. Zoo Biology 18: 111-127.

Pérez-Barbería, F.J. & Gordon, I.J. (2005). Gregariousness Increases Brain Size in Ungulates. Oecologia 145: 41-52.

Price, E.E. & Stoinski, T.S. (2007). Group Size: Determinants in the Wild and Implications for the Captive Housing of Wild Mammals in Zoos. Applied Animal Behaviour Science 103: 255-264.

Rees, P.A. (2002). Asian elephants (*Elephas maximus*) dust bathe in response to an increase in environmental temperature. Journal of Thermal Biology 27: 353-359.

Rees, P.A. (2004). Low Environmental Temperature Causes an Increase in Stereotypic Behavior in Captive Asian Elephants (*Elephas maximus*). Journal of Thermal Biology 29: 37-43.

Robitaille, J. & Prescott, J. (1993). Use of Space and Activity Budgets in Relation to Age and Social Status in a Captive Herd of American Bison, *Bison bison*. Zoo Biology 12: 367-379.

Sachser, N. Dürschlag, M., Hirzel, D. (1998). Social Relationships and the Management of Stress. Psychoneuroendocrinology 23: 891-904.

Saudargas, R.A. & Drummer, L.C. (1996). Single Subject (Small N) Research Designs and Zoo Research. Zoo Biology 15: 173-181.

Schmid, J. (1995). Keeping Circus Elephants Temporarily in Paddocks – the Effects on their Behaviour. Animal Welfare 4: 87-101.

Schenkel, R. & Schenkel-Hulliger, L (1969). Ecology and Behaviour of the Black Rhinoceros (*Diceros bicornis* L.): A Field Study. Paul Parney: Hamburg.

Schmid, J., Heistermann, M., Gansloßer, U., Hodges, J.K. (2001). Introduction of Foreign Female Asian elephants (*Elephas maximus*) into an Existing Group: Behavioural Reactions and Changes in Cortisol Levels. Animal Welfare 10: 357-372.

Schulte, B.A. (2000). Social Structure and Helping Behavior in Captive Elephants. Zoo Biology 19: 447-459.

Seidensticker, J. & Doherty, J.G. (1996). Integrating Animal Behavior and Exhibit Design. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 180-190.

Smith, R.L. & Read, B. (1992). Management Parameters Affecting the Reproductive Potential of Captive, Female Black Rhinoceros, *Diceros bicornis*. Zoo Biology 11: 375-383.

Spinage, C.A. (1994). Elephants. T & AD Poyser, Ltd: London.

Stoinski, T.S., Daniel, E., Maple, T.L. (2000). A Preliminary Study of the Behavioral Effects of Feeding Enrichment on African Elephants. Zoo Biology 19: 485-493.

Sukumar, R. (2006). A Brief Review of the Status, Distribution and Biology of Wild Asian Elephants, *Elephas maximus*. International Zoo Yearbook 40: 1-8.

Swaisgood, R.R. & Shepherdson, D.J. (2005). Scientific Approaches to Enrichment and Stereotypies in Zoo Animals: What's Been Done and Where Should We Go Next? Zoo Biology 24: 499-518.

Swaisgood, R.R., Dickman, D.M., White, A.M. (2006). A Captive Population in Crisis: Testing Hypotheses for Reproductive Failure in Captive-Born Southern White Rhinoceros Females. Biological Conservation 129: 468-476.

Thompson, K.V. (1996). Behavioral Development and Play. In: Wild Mammals in Captivity. D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lampkin (Eds). The University of Chicago Press: Chicago, pp. 352-371.

Veasey, J.S. (2006). Concepts in the Care and Welfare of Captive Elephants. International Zoo Yearbook 40: 63-79.

Veasey, J.S., Waran, N.K., Young, R.J. (1996). On Comparing the Behaviour of Zoo Housed Animals with Wild Conspecifics as a Welfare Indicator, Using the Giraffe (*Giraffa camelopardalis*) as a Model. Animal Welfare 5: 139-153.

Vidya, T.N.C. & Sukumar, R. (2005). Social and Reproductive Behavior in Elephants. Current Science 89: 1200-1207.

Wiedenmayer, C. (1998). Food Hiding and Enrichment in Captive Asian Elephants. Applied Animal Behaviour Science 56: 77-82.

Wiese, R.J. & Willis, K. (2004). Calculation of Longevity and Life Expectancy in Captive Elephants. Zoo Biology 23: 365-373.

Wiese, R.J. & Willis, K. (2006). Population Management of Zoo Elephants. International Zoo Yearbook 40: 80-87.

Wilson, M.L., Bloomsmith, M.A., Maple, T.L. (2004). Stereotypic swaying and serum cortisol concentrations in three captive African elephants (*Loxodonta africana*). Animal Welfare 13: 39-43.

Wilson, M.L., Bashaw, M.J., Fountain, K., Kieschnick, S., Maple, T.L. (2006). Nocturnal Behavior in a Group of Female African Elephants. Zoo Biology 25: 173-186.

Wittemyer, G. & Getz, W.M. (2007). Hierarchical Dominance Structure and Social Organization in African Elephants, *Loxodonta africana*. Animal Behaviour 73: 671-681.

Wyatt, J.R. & Eltringham, S.K. (1974). The Daily Activity of Elephants in the Rwenzori National Park, Uganda. East Africa Wildlife Journal 12: 273-289.