5-2006

Tapirs and Rhinoceroses in Captivity: An Examination of the North American Captive Populations and Their Husbandry

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TAPIRS AND RHINOCEROSES IN CAPTIVITY: AN EXAMINATION OF THE NORTH AMERICAN CAPTIVE POPULATIONS AND THEIR HUSBANDRY

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

2006

ABSTRACT

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by

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Utah State University, 2006

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Program: Ecology

All species of Tapiridae and Rhinocerotidae are threatened or endangered in the wild. Captive populations have been established for most of these species, but successful management has proved challenging. Effective ex situ conservation strategies, however, rely on the ability of zoological institutions to maintain and breed these endangered species. In this study, I examined the captive environment to identify the factors associated with reproduction, mortality, and health of rhinos and tapirs. Zoological institutions in the North American region that currently housed rhinos and/or tapirs were surveyed in 2003. Attaining an approximately 90% response rate, I compiled information on the following variables to describe the captive environment: number of enclosures, enclosure type, enclosure area, number of animals, public viewing, percent of walls surrounding the enclosure, enclosure substrate, topography, vegetation, mud wallows, pools, shelters, percent shade, climate, diet, feeding regime, time spent by keepers, and vaccinations. Information regarding the incidence of health problems also was obtained through the survey. Studbook data was used to obtain life history and demographic information.

Three species of tapirs [Baird's (*Tapirus bairdii*), South American (*T. terrestris*), and Malay (*T. indicus*)] and three species of rhinos [black (*Diceros bicornis*), white (*Ceratotherium simum*), and Indian (*Rhinoceros unicornis*)] were included in this study. Due to the small captive population sizes, genetic and demographic Allee effects were detected. While tapirs responded similarly to their captive environment, each rhino species responded differently. Both exhibit area and complexity were associated with the responses of captive tapirs and rhinos. Climate also was an influential factor for both groups of species. Other key factors included density, diet, keeper time, percent of public perimeter, and vaccinations. Complex interactions among the variables were found, including a nonlinear relationship between mean exhibit size and reproduction for black rhinos.

The results of this study can be used to improve the captive management of tapirs and rhinos. By identifying the patterns associated with successful reproduction, reduced mortality, and fewer health problems, we can move towards establishing self-sustaining populations for these species. This goal is critical for the continued husbandry and conservation of these species.

(130 pages)

ACKNOWLEDGMENTS

This research was made possible by the participating zoos and the support of the AZA Rhino TAG Chair, Evan Blumer; AZA Tapir TAG Chairs, Rick Barongi and Lewis Greene; and studbook keepers, Tom Foose, Joe Roman, Don Goff, and Jennifer McLain. Over 100 zoological institutions responded to the survey and I thank each and every one of them: Aalborg Zoo, Adelaide Zoo, Albuquerque Biological Park, Alexandria Zoological Park, Amneville Zoo, Audubon Zoo, BREC's Baton Rouge Zoo, Baltimore Zoo, Belfast Zoological Gardens, Bergen County Zoological Park, Birmingham Zoo, Blackpool Zoo, Branfere Animal and Botanical Park, Brevard Zoo, Brookfield Zoo, Buffalo Zoological Gardens, Busch Gardens, Caldwell Zoo, Cameron Park Zoo, Chaffee Zoological Gardens of Fresno, Cheyenne Mountain Zoo, Cincinnati Zoo, Cleveland Metroparks Zoo, Columbus Zoo and Aquarium, Dallas Zoo, Denver Zoological Gardens, Detroit Zoological Institute, Disney's Animal Kingdom, El Paso Zoo, Ellen Trout Zoo, Erie Zoo, Fort Worth Zoological Park, Fossil Rim Wildlife Center, Frankfurt Zoo, Franklin Park Zoo, Gladys Porter Zoo, Great Plains Zoo, Greater Vancouver Zoo, Hamilton Zoo, Hattiesburg Zoo, Henry Vilas Zoo, Honolulu Zoo, Houston Zoological Gardens, Jackson Zoological Park, Kansas City Zoo, Knoxville Zoological Gardens, Knuthenborg Park, Kyiv Zoo, Lee Richardson Zoo, Lion Country Safari Inc., Little Rock Zoological Gardens, Los Angeles Zoo, Louisiana Purchase Gardens and Zoo, Lowry Park Zoological Garden, Memphis Zoological Garden and Aquarium, Mesker Park Zoo, Miami Metrozoo, Miejski Ogrod Zoo, Milwaukee County Zoological Gardens, Minnesota Zoological Garden, Montgomery Zoo, Mountain View Conservation Centre, Nashville Zoo at Grassmere, Niabi Zoo, North Carolina Zoological Park, Oklahoma City Zoological Park, Omaha's Henry Doorly Zoo, Oregon Zoo, Parc Zoo de Mulhouse, Perth Zoological Gardens, Philadelphia Zoological Garden, Pittsburgh Zoo & Aquarium, Potter Park Zoological Gardens, Poznan Zoo, Racine Zoological Garden, Red McCombs Ranch, Reid Park Zoo, Riverbanks Zoo, Rolling Hills Refuge Wildlife Conservation Center, Saint Louis Zoological Park, San Antonio Zoological Gardens & Aquarium, San Diego Wild Animal Park, San Diego Zoo, San Francisco Zoological Gardens, Sedgwick County Zoo, Silver Springs Park, Singapore Night Safari, Singapore Zoological Gardens, Smithsonian National Zoological Park, Southwick Zoo, Taronga Zoo, Tel Aviv Zoological Center, Toledo Zoological Gardens, Toronto Zoo, Tulsa Zoological Park, Twycross Zoo, Utah's Hogle Zoo, Virginia Zoological Park, White Oak Conservation Center, The Wildlife Conservation Society/Bronx Zoo, Wildlife Safari Inc., Wildlife World Zoo, The Wilds/IRF, Woodland Park Zoological Gardens, The ZOO, Zoo Atlanta, and Zoological Garden Basel. Although too numerous to name, I am grateful to all the zoo staff that took the considerable time and effort to be a part of this project. The Utah State University (USU) College of Natural Resources Quinney Fellowship, USU Ecology Center, USGS Utah Cooperative Fish and Wildlife Research Unit, and Tapir Preservation Fund provided funding for this research.

Many people contributed to this research. Sheryl Todd at the Tapir Preservation Fund provided invaluable logistic support for which I am grateful. Laurie Bingaman Lackey deserves extra recognition and thanks for all her help with SPARKS studbooks and for always answering my countless questions. I also appreciate the assistance of Kathy Carlstead, Pam Dennis, Mary Wykstra, and the Aquarium and Zoo Facilities

Association (Facility Design Resource Notebook Project) who helped review the survey. Without all their help and support, this research would not have been possible.

I especially thank my advisory committee, Gary Belovsky, Michael Wolfe, Edward Evans, and James Powell, for their critical reviews, suggestions, and support throughout my doctoral program. I have enjoyed working with all of them and hold them in high regard. Gary Belovsky accepted the esteemed position of director of the University of Notre Dame Environmental Research Center but chose to remain on my committee, and for that, I am exceptionally appreciative. I also would like to thank Mark Ritchie and James Haefner for being a part of my doctoral program in its early stages. I am, however, particularly indebted to my major advisor, John Bissonette, for his endless and unwavering support, guidance, and encouragement. He was a constant source of inspiration and an extraordinary mentor. I consider myself incredibly lucky to have worked with such talented and gifted people.

This research is truly a symbol of the power of the human spirit. Lyme disease may have robbed me of time, but not my determination to overcome the odds and succeed. This achievement, however, was not accomplished alone. To all of the aforementioned names, family, friends, and colleagues, I extend heartfelt thanks. My parents in particular deserve special acknowledgment. Thank you for always being by my side, listening, encouraging, helping, supporting, and loving me through it all. My gratitude is immeasurable.

Lisa A. Nordstrom

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CHAPTER 1

INTRODUCTION

Environmental conditions and resources affect an organism's growth, reproduction, health, and survival [Begon et al., 1990]. In zoological parks, enclosures provide the environment in which captive animals live. Only under optimal conditions will an organism be able to maximize its fitness. To some degree, fitness is anthropogenically controlled in zoos. Yet captive animals may still have lower productivity due to inadequate living conditions, dietary deficiencies, limited mating choices, or other factors [Hediger, 1965; Mellen, 1991; Smith and Read, 1992]. However, few data exist on the relationship between the captive environment and reproduction, mortality, and health. As a consequence, curators have little scientific information to base husbandry requirements for captive species [Seidensticker and Doherty, 1996; Carlstead, 1999].

Successful husbandry is important for the establishment of effective ex situ conservation strategies. Wildlife populations are increasingly threatened with the risk of extinction [Pimm et al., 1995; Rosser and Mainka, 2002]. Zoos can provide a safeguard against the total extinction of a species through captive breeding and reintroduction programs [Cohn, 1988; Ryder, 1997; Swaisgood, 2004a, b]. While captive breeding alone cannot solve the problems of species extinctions, The World Conservation Union (IUCN) views captive breeding programs as complementary to in situ efforts [Emslie and Brooks, 1999] and recommends that ex situ conservation be initiated before population sizes become too small to establish viable captive populations [Swaisgood, 2004a, b].

Once established, viable, self-sustaining captive populations eliminate the need to remove individuals from endangered populations in the wild. Unfortunately, captive breeding is often a difficult task, fraught with many problems and failures due to an insufficient understanding of the target species, as well as suboptimal conditions in the captive environment [Swaisgood, 2004a]. In order for captive breeding to be successful, zoological institutions need to know the species' environmental, housing, dietary, medical, social, and behavioral requirements to determine proper husbandry [Kleiman, 1980; Mellen, 1994; Swaisgood, 2004a]. Thus, there is an urgent need for scientific research to provide solutions for the effective conservation of captive species, particularly when conservation strategies in the wild fail to result in stable populations.

The philosophy on the role of zoos has undergone many changes in recent decades [Gibbons et al., 1995; Hutchins and Conway, 1995; Hutchins et al., 1995; Mench and Kreger, 1996]. Historically, little consideration was given to the animals' well-being or ex situ conservation. Zoological exhibits basically consisted of square, kennel-like cages [Hediger, 1950; Seidensticker and Doherty, 1996]. Today, there is greater emphasis on conservation research, education, endangered species management, standards of animal care, and enclosure design [Hutchins and Conway, 1995; Hutchins et al., 1995, Kleiman et al., 1996; Swaisgood, 2004a]. Demographic and genetic management of captive populations are now integral parts of ex situ conservation programs established for species [Ballou and Foose, 1996; Earnhardt et al., 2001]. The typical square cages also have been transformed into more naturalistic exhibits [Gibbons et al., 1994; Forthman et al., 1995]. Unfortunately the redesign of enclosures is usually based on assumptions and aesthetics, rather than on empirical data concerning the biology and behavior of the organism [Carlstead, 1999]. This lack of knowledge has led to numerous problems for the care of captive animals, including inadequate reproduction, health problems, and mortality. For example, captive management of rhinoceros remains problematic, with productivity levels below demographic and genetic sustainability, for unknown reasons [Smith and Read, 1992; Fouraker and Wagener, 1996; Carlstead, 1999; Carlstead et al., 1999; Emslie and Brooks, 1999; AZA Rhino Advisory Group, 2002].

Enclosures contain many different features that could affect the captive animal. At the basic level, the enclosure must contain at least adequate food, water, shelter, and space. However, the natural history, social behavior, mating systems, and other ecological requirements of species also need to be taken into account. Burghardt [1975] categorized the variables operating in a zoo environment into five main factors: the enclosure, husbandry procedures, keepers, public visitors, and the organism. The combination of these factors defines the captive environment and the response of the organism, ultimately determining its health, reproduction, and survival.

Debate currently exists regarding the relative importance of enclosure size and structural complexity for captive animals. Hediger [1950] asserted that enclosure size should be based on flight distances of the wild animal in captivity, but that tame animals only need enclosures that are several times the length of their bodies to satisfy their physiological needs. Indeed, the quality of space, rather than quantity, is assumed to be more important for the management of captive species [Hediger, 1950; Besch and Kollias, 1994]. However, some species, such as rhinos, are known to have large spatial requirements, which scale allometrically with body size [McNab, 1963]. Evidence also appears to indicate that wide-ranging carnivores respond negatively to captivity [Clubb and Mason, 2003]. Fueling the debate between enclosure size and complexity are discrepancies between research results; several studies have found that enclosure size is insignificant [Wilson, 1982; Mellen, 1991; Kreeger et al., 1996; Lyons et al., 1997], while others have found it to be correlated with reproductive success and mortality [McCusker, 1978; Miller-Schroeder and Paterson, 1989; Roberts, 1989; Carlstead et al., 1999]. The differences in enclosure size significance may be due to species perceptions and mobility. Species that are able to climb or fly would tend to view a more three-dimensional, rather than two-dimensional surface [Holling, 1992]. Scale domains that encompass relevant ecological processes also may create discontinuities or thresholds in species response to enclosure size [Holling, 1992]. For instance, breeding success may increase and mortality decrease as exhibit size increases, until a threshold is reached. Beyond this threshold, enclosure size may no longer be a significant factor.

Furthermore, the importance of size and complexity are not mutually exclusive, but may both influence species response. Miller-Schroeder and Paterson [1989] found that area, volume, and structural complexity were all associated with breeding success for gorillas. Increasing complexity may actually offset the potential effects of small exhibit sizes by increasing usable surface area or providing refuge areas within the enclosure. Conversely, animals kept in simple, sterile environments tend to have decreased health, lower reproduction, impaired brain and neural functioning, and more abnormal behaviors compared to those in enriched environments [Rosenweig and Leiman, 1968; Rosenweig et al., 1978; Carlstead, 1996; Kempermann et al., 1997; ILAR, 1998; Brown et al., 2003; Dukas and Mooers, 2003; Marashi et al., 2004]. By adding particular attributes within enclosures, such as mud wallows, pools, shade, or grass substrate, the captive environment may more closely meet the specific biological needs of a species.

Density also can influence reproduction and mortality, as a result of negative density dependent processes or Allee effects. Increasing the number of individuals reduces the relative amount of space for each individual within the enclosure and increases competition among individuals. Since tapirs and rhinos, excluding the white rhino, are primarily solitary, multiple males or females may lower breeding success and increase mortality. For example, Carlstead et al. [1999] found that zoos with a single black rhino female had a higher reproductive rate compared to zoos with multiple females, and that the mean age of first reproduction was significantly lower for those single female rhinos.

In the captive environment, stress can be a major factor for animals. Carlstead et al. [1999] found a correlation between mortality and the percent public access. Increases in the amount of public access along the enclosure perimeter may increase fear and stress for individuals in the enclosure. Chronic stress has been shown to have serious negative physiological and behavioral effects on individuals, which can impact the viability of captive populations [Carlstead, 1996]. Similar to public presence, keepers also may be a source of stress, particularly because of the close proximity between animals and keepers. The amount of time spent per day by keepers may be a useful measure of the response of tapirs and rhinos to humans.

In addition, diet and feeding regimes are known to impact the health of animals. Inadequacies in diet can lead to reduced reproduction and higher mortality rates [Asa, 1996; Fouraker and Wagener, 1996]. Improper nutrition also can create health problems, such as nutrient deficiencies, colic, or various disease syndromes [Fouraker and Wagener, 1996]. Furthermore, the conditions in zoological institutions are often conducive to the transmission of diseases among individuals [Dobson and May, 1986; Lafferty and Gerber, 2002]. High densities in captivity, exposure to other species, poor nutrition, and increased stress can increase the susceptibility of individuals to infectious agents [Dobson and May, 1986; Hinshaw et al., 1996; Lafferty and Gerber, 2002]. Preventive medical treatments, such as vaccinations, can help reduce the chance of disease outbreaks that jeopardize captive populations [Hinshaw et al., 1996].

Lastly, climate may have an effect on captive species when species adapted to a tropical/subtropical environment are kept in the temperate climate of North America. Temperature and precipitation can affect reproduction and survival if conditions are beyond species tolerance limits [Begon et al., 1990]. Furthermore, the amount of time that the animals are kept in the indoor enclosure will most likely be correlated with climate, with the zoos in the higher latitudes unable to provide outdoor access during the winter months.

The American Zoo and Aquarium Association (AZA) Minimum Husbandry Guidelines recommend standards for the management of species, including specifications for indoor and outdoor facilities, enclosure features, sanitation, diet, social groupings and veterinary care. Unfortunately, few scientific data exist on which to base these guidelines. For instance, AZA Minimum Husbandry Guidelines recommend that each adult tapir have an outdoor enclosure of at least 18.6 m^2 [Barongi, 1997]. However, whether this is the optimal size is unknown. Innis et al. [1985] suggest that the appropriate enclosures size can be calculated using the number of animals and the minimum preferred distances between individuals for a particular species. How to determine the preferred distance between individuals, however, is unclear, which could lead to potentially erroneous enclosure size calculations. Comparisons between the AZA suggested appropriate enclosure sizes and results from research studies on the actual effects of enclosure size could prove useful for developing better guidelines and models for calculating spatial requirements. This approach, using empirical data, could be applied to all of the factors that define the captive environment. By measuring environmental factors across multiple zoos and determining species response, the reliability of these guidelines may be improved, increasing the chance of success for captive management and conservation of threatened and endangered species.

STUDY ORGANISMS

Tapirs and rhinos were selected for this study for several reasons: (1) their worldwide threatened and endangered status; (2) presence in zoological institutions; (3) locomotory abilities, which affect their perception of the environment as a two-dimensional surface; (4) size differences between the two taxonomic families; (5) similarity in trophic level and digestive morphology; (6) social behavior, all being primarily solitary except for the white rhino; and (7) taxonomic relatedness, both members of the Order Perissodactyla. Captive management of tapirs, especially the Malay (*Tapirus indicus*) and lowland (*T. terrestris*) species, has been fairly successful in recent years, despite their threatened and endangered status in the wild [Barongi, 1993; Barongi, 1997]. The worldwide captive population of Baird's tapir (*T. bairdii*) remains low though, compared to the Malay and lowland tapirs [Barongi, 1993]. Reproduction among tapirs, however, is fairly commonplace, despite medical and behavioral problems that occur mainly due to lack of experience and knowledge [Barongi, 1997]. Conversely, rhinos have experienced numerous problems in captivity, resulting in the lack of self-sustaining populations for several species [Smith & Read, 1992; Carlstead, 1999; Carlstead et al., 1999; AZA Rhino Advisory Group, 2002]. Successful reproduction is a major problem for white rhinos (*Ceratotherium simum*), whereas high mortality is problematic for the black rhino (*Diceros bicornis*) in captivity [AZA Rhino Advisory Group, 2002]. The captive population of Indian rhinos (*Rhinoceros unicornis*) has fewer demographic problems, but its genetic diversity is low and many individuals are afflicted with foot problems [AZA Rhino Advisory Group, 2002]. The environment provided for each of these species may have a significant effect on reproduction, mortality, and health and needs to be further examined.

OBJECTIVES

The main objectives of this research are to assess the relationship between the captive environment and response of rhinos and tapirs. Reproduction, mortality, and health were used as the response variables. The frequency of health problems may provide a more sensitive measure of the effect of enclosure attributes on these species, considering that individuals in poor health are less likely to reproduce and more likely to die. The factors that are correlated with the response variables may vary among species, but the following descriptive variables were predicted to be biologically significant: exhibit size, animal groupings and density, overall enclosure complexity, enclosure attributes such as mud wallows, pools, shade, and substrate, the percentage of enclosure perimeter open to public access, time spent by keepers, diet, number of feedings, preventative medical treatments, and climate. Each of these variables and their interactions can impact the well-being of rhinos and tapirs, as previously described. Empirical data on husbandry and environmental factors across multiple zoos were acquired through a survey of North American zoos currently housing rhinos and tapirs. Studbook data was used to provide demographic information for each species at each zoo. Although individual behavior is an important aspect to be considered, this research only addressed how behavior translated into reproduction, mortality, and health.

Knowledge of how the captive environment affects rhinos and tapirs can be applied to improve captive management, as well as to provide a better understanding of rhinos and tapirs themselves. Human intervention and individual behavioral differences among animals, along with other factors that cannot be accounted for, may have affected the results of this study. Furthermore, because the data obtained are observational, only correlations between factors can be demonstrated. However, identifying the relationship between environmental factors and demographic and health parameters is a fundamental step for further developing successful management programs for rhinos and tapirs in captivity. One of the primary goals of the AZA Species Survival Plan for Rhinoceros is the "improvement of captive husbandry and management through research in health, nutrition, behavior, and reproduction to facilitate development of viable populations ex situ..." [AZA Rhino Advisory Group, 2002; p. 8]. The AZA Tapir Taxon Advisory Group (TAG) also has established similar objectives. This comprehensive, and largely exploratory, study fulfills that objective and provides much needed information for captive management of tapirs and rhinos. Consequently this research was approved by both the Rhino and Tapir TAG.

The following chapters address the relationship between the captive environment and species response for tapirs and rhinos, indicate important trends for reproduction, mortality, and health in the captive environment, and identify possible explanatory factors that need further investigation. Chapter 2 examines these topics for the family Tapiridae. Individual species responded similarly to their captive environment and consequently were analyzed as a group. Chapter 3 focuses on three individual species of rhinos, each responding slightly differently to their captive environment. Finally, chapter 4 compares and synthesizes the major results for each of these groups.

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CHAPTER 2

TAPIRS IN CAPTIVITY

INTRODUCTION

Tapirs qualify as a charismatic megavertebrate (i.e., large, interesting animals that could serve as a flagship species for conservation efforts [Cohn, 1988]), yet they have received relatively little scientific or public attention [Barongi, 1993; Janssen et al., 1996; Brooks et al., 1997]. Despite their large size and unique morphology, these animals remain ecologically and publicly obscure. In a study of visitor reactions to tapir exhibits at zoos, Seitz [2001] found that tapirs were misidentified as 86 different animals. Tapirs are among the largest mammals in the neotropics, but can go unnoticed due to their solitary lifestyle, crepuscular/nocturnal behavior, and habitat preference for moist areas in tropical forests. This also makes them particularly difficult to study, resulting in a lack of information regarding their distribution, population dynamics, and basic biology. Despite their long history in zoos, potentially extending back to 1704 in Europe [Kourist in Padilla and Dowler, 1994], there is also a paucity of research of tapirs in captivity. Unfortunately, all tapir species are threatened with extinction, creating an imperative need for research, both in the wild and in captivity.

Related to rhinos and horses in the order Perissodactyla, tapirs belong to the family Tapiridae, which consists of four extant species: Baird's (*Tapirus bairdii*), South American (*T. terrestris*), mountain (*T. pinchaque*), and Malay (*T. indicus*) tapir. The Baird's, South American, and mountain tapirs occur in the neotropics, whereas the Malay tapir's range is in southeast Asia (Fig. 2-1). All four species have similar life histories, behavior, and ecological requirements [Barongi, 1993]. Adult tapirs range in size from 200-450 kg, with the Malay tapir being the largest and the mountain tapir, the smallest [Barongi, 1993; Janssen et al., 1996]. Like most large mammals, tapirs have a low reproductive rate, with usually only a single calf produced after approximately 13 months gestation [Read, 1986; Barongi, 1993; Padilla and Dowler, 1994; Brooks et al., 1997]. Tapirs are herbivorous and eat a variety of browse, grasses, and fruit [Williams and Petrides, 1980; Bodmer, 1990; Barongi, 1993; Padilla and Dowler, 1994; Brooks et al., 1997; Henry et al., 2000; Downer, 2001]. Their elongated proboscis aids in foraging and provides them with an acute sense of smell [Barongi, 1993; Padilla and Dowler, 1994; Brooks et al., 1997]. Rivers, lakes, or other water sources are frequently used by tapirs, who are commonly found swimming or using mud baths [Barongi, 1993; Padilla and Dowler, 1994]. Although Baird's tapirs use both primary and secondary forest habitat [Foerster and Vaughan, 2002], limited evidence suggests that Malay tapirs prefer undisturbed forest habitat [Williams and Petrides, 1980; Medici et al., 2003].

Many of these traits have made tapirs particularly vulnerable to extinction. They are federally listed as endangered species, although the lowland and Malay tapirs are categorized as vulnerable, and only Baird's and mountain tapirs as endangered under The World Conservation Union (IUCN) Red List [AZA Tapir TAG, 2004; IUCN, 2004]. The main threats are habitat loss across their entire range and hunting particularly in Central and South America [Janssen et al., 1996; Brooks et al., 1997; Medici et al., 2003]. Overexploitation of tapir populations can occur at even low levels of extraction, due to their low population growth rate capacity and low densities across their range [Brooks et al., 1997; Medici et al., 2003]. Home range size can vary from approximately 1 km^2 in optimal habitat to 12.75 km^2, with densities ranging from 0.035-1 individual per km^2 [Williams and Petrides, 1980; Brooks et al., 1997; Foerster and Vaughan, 2002; Medici et al., 2003]. Consequently, large areas of habitat are required to maintain sustainable populations. Fragmentation further exacerbates the effects of habitat loss and hunting, increasing the chances for local extinction. If current rates of deforestation continue, the Malay tapir in Sumatra is predicted to go extinct within 50 years or less, regardless of its current population size, which is estimated between 900 and 3,000 [Medici et al., 2003]. The mountain tapir is the most critically endangered, with only 2,500 individuals or less, and may become extinct within the next two decades given current habitat destruction and hunting pressures [Brooks et al., 1997; IUCN, 2004]. Currently all four species of tapirs are decreasing in number [IUCN, 2004]. In situ conservation, in conjunction with ex situ efforts, is needed to help protect these decreasing populations.

In general, tapirs are successfully bred and managed in captivity, with similar husbandry for all tapir species [Barongi, 1993, 1997, 2003; Shoemaker et al., 2003]. The captive populations of Baird's and Malay tapirs have been designated as a part of the American Zoo and Aquarium Association (AZA) Species Survival Plan, requiring a captive breeding program and management to preserve genetic diversity and demographic sustainability [AZA Tapir TAG, 2004]. Genetic diversity of captive populations is limited by the number and heterozygosity of the wild-caught founders and their fitness. Maintaining this limited genetic diversity can be challenging due to the small population sizes and need for long-term management [Ballou and Foose, 1996]. However, loss of genetic diversity through inbreeding and genetic drift can have profound effects on species viability and suitability to be reintroduced back into their native range [Allendorf and Leary, 1986; Gilpin and Soulé, 1986; Ballou and Foose, 1996]. Increasing captive population sizes can reduce their vulnerability to genetic losses and extinction [Gilpin and Soulé, 1986; Ballou and Foose, 1996], but limitations on available space generally preclude sizable populations [Earnhardt et al., 2001]. In order to achieve larger population sizes, only two tapir species, Baird's and Malay, were chosen as the primary focus of the North American captive tapir management program, although all four species have been exhibited [AZA Tapir TAG, 2004].

Husbandry and medical problems of tapirs have been attributed mainly to lack of knowledge concerning basic biology and individual variation [Barongi, 1993, 1997, 2003; Shoemaker et al., 2003]. Janssen et al. [1996] found that the primary health problems were noninfectious gastrointestinal diseases and infectious respiratory diseases (e.g., pneumonia, tuberculosis). Once a major problem with a high incidence rate [Barongi, 1993], rectal prolapse has become less common in captive tapirs [Janssen et al., 1996]. This is potentially due to improvements in husbandry, diet, and the captive environment, although the effect of these factors on North American captive tapirs has not been evaluated.

As in natural habitat, captive environments can have profound effects on reproduction, health, and survival of individuals. Although husbandry standards have been established, scientific studies examining the effects of husbandry practices and enclosure design are lacking. The relative importance of size versus complexity of enclosures has been a debated issue in captive management. Hediger [1950] first asserted that the quality of space (i.e., the characteristics that define the animal's living space) is more important than the total area. Research results, however, are equivocal. Positive relationships with reproduction and enclosure size have been reported (e.g., black rhinos (*Diceros bicornis*) [Carlstead et al., 1999]), as well as no relationship between enclosure size, nor complexity, with reproductive success (e.g., small felids [Mellen, 1991]). Disturbances outside the enclosures, such as public presence and transfers of individuals into and out of zoological institutions, also may affect the health and fitness of tapirs. In the wild, tapirs tend to avoid areas with increased human disturbances, either spatially [Tobler, 2002] or possibly through shifts in temporal patterns of activity [Foerster and Vaughan, 2002]. Disturbances can increase stress, which may cause abnormal behaviors and physiological changes that reduce reproduction and increase mortality and health problems [Carlstead, 1996]. Carlstead and Brown [2005] found that chronic stress may be caused by exposure to zoo visitors, interactions with keepers, and intraspecific social relationships for rhinos, which may negatively influence captive white (*Ceratotherium simum*) and black rhino populations. Furthermore, temperature and humidity have long been known to affect breeding success [Hediger, 1965] and disease susceptibility [Besch and Kollias, 1994] of captive animals. The climate in North American zoos may influence tapir reproduction and health, especially considering that all tapir species are associated with tropical environments.

Understanding how these environmental factors may affect tapirs could be applied to improve captive management of tapirs. If husbandry standards are indeed "the foundation for any program of successful and humane tapir management" [Shoemaker et al., 2003], captive management research is instrumental for attaining tapir management goals. The objectives of this study were to assess the reproduction, mortality, and health of North American captive tapir populations and to identify relationships with husbandry and enclosure attributes.

METHODS

All four species of tapirs (i.e., Baird's, South American, mountain, and Malay) were included in this study. The International Central American (Baird's) Tapir Studbook [Roman, 2005], North American Regional South American Tapir Studbook [Goff, 2005], and International Malay Tapir Studbook [McLain, 2005] were used for life table information for each species. A studbook, containing the history of each individual in the captive population, has not been established for the mountain tapir. Data on birth origin, rearing type, number of years housed within a zoo, and number of transfers between zoos also were obtained from studbook data. Institutional summary reports were created using the Single Population Analysis and Records Keeping System (SPARKS) [ISIS, 2004]. Demographic analysis, including calculations of population growth rate, genetic diversity, and mean inbreeding, was performed using Population Management 2000 [Pollak et al., 2005].

In addition, I conducted a census of all North American zoos housing tapirs. Using the International Species Information System (ISIS) Species Holdings [ISIS, 2003], I identified 52 institutions in the United States and Canada currently housing tapirs. In 2003, I mailed a questionnaire to these zoological institutions to gather information on enclosure attributes and management practices. The American Zoo and Aquarium Association (AZA) Tapir Taxon Advisory Group (TAG) approved this survey [Barongi, pers. comm.] and a letter of support was included with the survey forms. A nearly 90% response rate was achieved. Variables on the survey that were used in analyses included: number of enclosures, total enclosure area, percent of public access along enclosure perimeter, enclosure substrate, topography, percent shade, amount of vegetation, number of water pools and mud wallows, diet, and frequency of health problems.

Climate for each zoo was determined using climatic data from the National Climatic Data Center [2004] and Utah Climate Center [2005]. I used the nearest weather stations to each institution to obtain data on the mean number of days with a minimum temperature of 32° F or lower, mean number of days with a maximum temperature of 90° F or higher, mean annual temperature, standard deviation of normal daily mean temperature, and the mean normal precipitation, including the liquid water equivalent of snowfall. Density was calculated by dividing the number of living animals at an institution by the total main exhibit area. An index of complexity was generated using the number of attributes within the enclosure and a ranking of topography, with level being ranked lowest and hills highest. Attributes included the presence of trees, shrubs, pools, mud wallows, and shelters. Mortality for each species at an institution was calculated by dividing the total number of deaths by the number of individuals held at the institution and by the total number of years that each species was housed, in order to standardize across institutions (i.e., Mortality rate = $\frac{\#deaths}{[N(tapirs) \cdot \#years]}$). For example, a zoo housing 5 Baird's tapirs over 15 years with 2 deaths during that period would have a mortality rate of 0.0267. Reproductive rate was similarly determined by dividing the total number of births, regardless of survival of the young, by the number of females held at the institution and by the total number of years housed (i.e., Reproductive rate = $\frac{\#\,births}{[N(females)\cdot \#\,years]}$). Reproduction was calculated only for institutions that held at least one potential breeding pair. Health problems were grouped into the following categories: foot, eye, skin, dental/oral, respiratory diseases, colic, chronic diarrhea or vomiting, hemolytic anemia, parasitic infections, rectal prolapse, vasculopathies, and stereotypic behavior. The overall, combined health at a zoological institution was measured using the occurrences of each health problem, weighted by its frequency rank of common, rare, or no occurrences.

This was primarily an observational and exploratory study, examining the relationships among the response variables (i.e., reproduction, mortality, and frequency of health problems) with the various husbandry and captive environment variables. Because of this, cause and effect relationships cannot be demonstrated, but rather correlations were identified that need further examination. Identifying the model that best described the data was the primary objective.

Data analysis was performed using SAS [SAS Institute, 2003] and JMP IN [SAS Institute, 2004]. Data were pooled across all tapir species, unless there were significant differences between species. Summary statistics were calculated for each of the explanatory variables and correlations among variables were analyzed. Categorical data analysis was performed to assess differences in life history traits between species, sex (male or female), birth origin (wild or captive born), rearing type (parent or hand reared), and number of transfers between zoos. Kruskal-Wallis tests were used due to skewed, nonparametric distributions.

A principal components analysis was used for highly intercorrelated climatic variables. The first two principal components for climate described 81% of the variation (Table 2-1). The first component (w1) was characterized by higher mean annual temperature, fewer days below freezing, and less annual variation in temperature. The second component (w2) was primarily a moisture variable, with decreasing precipitation and increasing days above 90° F.

Multiple linear regression models (70 total) for reproduction, mortality, and health were constructed to evaluate four main effects: enclosure size, complexity, disturbance, and climate. Size effect included three variables: total number of enclosures (N), density (D), and the coefficient of variation of enclosure area (Acv). The percent variation in area served as a measure of difference between smaller night quarters or holding areas and the larger main exhibit areas. This difference in enclosure sizes may be important for captive tapirs since animals are kept indoors during inclement weather. An index of complexity (C), measuring the amount of heterogeneity within the enclosure, was used to assess a complexity effect. Disturbance effect consisted of the number of transfers per year (T) and the percent of public access along enclosure perimeter (P). Climate included the first two principal components (w1, w2; Table 2-1). Akaike weights, calculated from Akaike's information criterion corrected for small sample size (AIC_c), were used to rank the models and the relative importance of the explanatory variables [Burnham and Anderson, 2002]. Evidence ratios were used to further evaluate the models in the set.

In addition, health was investigated using polytomous ordinal logistic regression to examine the most common health problems reported on the zoological survey. Skin problems were predicted to be associated with drier climate, fewer water variables (i.e., pools, mud wallows, and showers), and less complexity. Topography and substrate were primarily thought to influence foot health, although exhibit area, complexity, and climate also were examined. Eye problems were predicted to be a negative function of percent enclosure shade and warmer climates. Lastly, relationships between dental/oral health and diet and number of feedings were analyzed.

RESULTS

Studbook Analysis

The North American captive tapir populations are relatively small (Table 2-2). The entire captive mountain tapir population (N = 6) is in North America [AZA Tapir TAG, 2004], making it very rare in captivity, as well as in the wild. The captive tapir populations have increased in size from a small number of wild-born founders, reaching a maximum of 38 Baird's, 96 South American, and 61 Malay tapirs (Fig. 2-2). The Baird's tapir has the fewest number of founders, and consequently the lowest genetic diversity and highest mean inbreeding compared to the South American and Malay tapirs (Table 2-2). The maximum number of Baird's, South American, and Malay combined was 159 individuals in 1993. The current captive tapir populations are entirely captive born (Fig. 2-2).

Demographic analysis of the Baird's, South American, and Malay tapir studbooks shows stable population growth ($\lambda \approx 1$), with nearly equal sex and age distributions (Table 2-2). Life history traits, including fecundity and survivorship, are similar between tapir species (Table 2-2, Fig. 2-3). Fecundity appears erratic, but it is not an accurate estimate or model of true fecundity due to small sample sizes in each age class. No seasonality of reproduction was found, with births occurring year-round. Of 556 births recorded across all three species, only 2 birth events from South American tapirs had a litter size of 2, with the rest composed of only 1 calf. Nearly all recorded tapir rearings across all species (n = 923) were by the parent (88%, n = 816), with less than 3% by hand (n = 24).

The age of first birth was similar for all three tapir species, but differed between birth type, with wild born females giving birth later, on average, than captive born females (8.4 vs. 7.0 years, $\chi^2 = 5.66$, 1 df, P = 0.02). Mean interval between births was slightly lower for South American tapirs compared to Baird's and Malay tapirs ($\chi^2 = 11.97$, 2 df, $P < 0.01$; Table 2-2). However birth intervals did not significantly differ between birth origin (i.e., wild or captivity). The number of births varied between species, with the Baird's tapir having more offspring than the South American or Malay tapirs ($\chi^2 = 7.79$, 2 df, P = 0.02; Table 2-2). Controlling for species, no significant differences were found between birth origin or sex on the number of births. The number of transfers between zoos did not appear to influence individual reproduction.

Longevity, however, did differ between number of transfers, with mean longevity slightly increasing with the number of transfers ($\chi^2 = 269.5$, 3 df, $P < 0.0001$). The relationship held when individuals living less than one year were excluded from the analysis ($\chi^2 = 32.58$, 3 df, $P < 0.0001$). The mean longevity for adult individuals never transferred, transferred a single time, transferred 2 times, and transferred 3 or more times were approximately 8.6, 8.7, 10.9, and 15.6 years, respectively. No significant differences were found between species, sex, or birth origin for longevity. Mortality of offspring within the first year after birth represents over one quarter of tapir mortality, with mortality within the first thirty days comprising the majority of these deaths (Table 2-2).

Zoological Survey

No significant differences were found among species for reproductive or mortality rate (Table 2-3). Consequently, regression models included all tapir species in the analysis. Table 2-4 summarizes the mean and variation of the variables used in the models, excluding climate principal components 1 (w1) and 2 (w2).

Reproduction was found to be a function of number of transfers per year, number of enclosures, and complexity (Table 2-5; Fig. 2-4). Considerable model selection uncertainty exists, with no single best model, shown by the low Akaike weights. However, using multimodel inference to rank the explanatory variables, only the number of transfers per year was relatively important, compared to the other variables (Table 2-6). As transfers per year increase, birth rate at a zoo also increases. The number of enclosures and complexity index also were moderately important, both showing slightly positive relationships with reproduction.

None of the models adequately explained the variation in mortality, with the null model ranked highest (Table 2-5). Upon further examination using nonparametric correlation analysis, mortality was found to be positively correlated with health problems (Spearman's Rho = 0.254, P = 0.08).

The most common health problems were skin, foot, eye, and oral (Table 2-7). Regression analysis revealed a relationship between weighted frequency of health problems and percent perimeter of public access, density, and the coefficient of variation of enclosure areas (Table 2-5). Similar to the reproduction model analysis, no single model best explained the health problems data. Percent perimeter of public access ranked highest in relative importance, with density and coefficient of variation of area ranked next highest (Table 2-6). Health problems were a negative function of public perimeter and coefficient of variation of area, but a positive function of density (Fig. 2-5). One outlier, corresponding to a zoo with a small main exhibit (~70 m^2) with three Malay tapirs kept separate, was identified for density. However, removing this outlier did not significantly change the relationship between health problems and density (Fig. 2-5). The combined model including public perimeter, density, and coefficient of variation of area was added to the model set for exploratory data analysis. However this model did not explain the data better than the "best" model. The combined model was ranked second in the model set, but was approximately equivalent to the density and perimeter model with an evidence ratio of 1.16 (i.e., nearly 1:1).

Examining specific health problems revealed species differences for eye and skin problems. Malay tapirs tend to have a greater frequency of eye problems, while Baird's tapirs have a lower frequency of skin problems (Table 2-7). Skin health was associated with mud wallows ($G^2 = 6.77$, 1 df, $P < 0.01$), but not with climate, complexity index, pools, or number of showers. Zoological enclosures with more mud wallows tended to have tapirs with fewer skin problems. A relationship between enclosure shade and eye health was not found. However a relationship between climate (w1) and eye health was identified ($G^2 = 3.19$, 1 df, $P = 0.07$), with zoos located in warmer climates experiencing more eye problems. Foot problems also were a function of climate (w1: $G^2 = 12.02$, 1 df, $P < 0.01$; w2: $G^2 = 3.37$, 1 df, $P = 0.07$), along with exhibit area ($G^2 = 5.40$, 1 df, P =

0.02). Zoos in warmer, wetter climates with large enclosure sizes had fewer foot problems reported. Excluding climate and exhibit size as explanatory variables, complexity index became important for explaining foot health ($G^2 = 5.47$, 1 df, $P = 0.02$). Interestingly, there is a positive correlation between complexity index and main exhibit area (Spearman's Rho = 0.3461, P = 0.01) and warm climates (w1: Spearman's Rho = 0.3903, P < 0.01). Substrate and topography, while a factor of complexity, did not reveal a relationship with foot health. No relationship was found between oral health problems and diet or number of feedings.

DISCUSSION

Captive management of tapirs has made great strides in the last two decades. International and regional studbooks were created [Barongi, 1993], establishing a record for each individual in the captive population and a database for demographic and genetic analyses. In 1991, the AZA Tapir TAG was formed "to enhance conservation initiatives for all species of tapir in the wild and in captivity" [AZA Tapir TAG, 2004]. AZA minimum husbandry guidelines for all four tapir species were printed in 1997 and recently updated in 2003 [Barongi, 1997, 2003]. More thorough tapir husbandry standards, covering all aspects of abiotic (e.g., temperature, shade, space) and biotic (e.g., social grouping, diet) conditions in captivity, also were developed in 2003 [Shoemaker et al., 2003]. Following the first International Tapir Symposium in 2001, The IUCN Species Survival Commission (SSC) Tapir Specialist Group (TSG) established a Zoo Committee, to facilitate coordination among international institutions. Most recently, the AZA Tapir TAG, with IUCN/SSC TSG, created a North American Regional Collection

Plan (RCP), approved by the AZA's Wildlife Conservation and Management Committee in 2004. The RCP delineates captive management recommendations based on demographic and space analyses and conservation status of the taxon. The IUCN/SSC TSG is currently working on updating an international tapir conservation action plan (original published in 1997 [Brooks et al., 1997]), which also will be incorporated as a part of the RCP.

Captive tapir species in North America have remarkably similar life history traits and are now entirely captive born. Although the North American captive populations for each tapir species, excluding the mountain tapir, are self-sustaining [AZA Tapir TAG, 2004], the populations are not sufficient for long-term viability, in terms of population persistence and the maintenance of genetic diversity above a 90% threshold, without new individuals [Barongi, 2003; Lewis Greene, pers. comm.]. Currently, the North American captive tapir population has a greater percentage of Baird's tapir, but fewer South American tapirs compared to the composition of the worldwide captive population, which is composed of approximately 50% lowland, 40% Malay, and 10% Baird's [Barongi, 1993]. The total captive carrying capacity for tapirs in North America was estimated to be approximately 150, constraining target population sizes for the Baird's and Malay to 75 individuals each [AZA Tapir TAG, 2004]. There was a moratorium placed on breeding South American tapirs in 1996 [Janssen et al., 1996] and the current captive population is being phased out because of space limitations in zoological institutions and their lower conservation status [AZA Tapir TAG, 2004].

Given historical captive tapir population trends (Fig. 2-2), 150 total individuals is a reasonable estimate of current space availability for tapirs in North America. However, target population sizes of 75 individuals are still relatively small and will require intensive management to maintain viable populations. Small populations are particularly vulnerable due to random variation in birth and death rates and loss of genetic variability [Gilpin and Soule, 1986; Belovsky et al., 1994]. Earnhardt et al. [2001] found that increases in current population size, target population size, and mean generation time have little effect on time to the 90% viability risk threshold when populations have genetic diversity levels already close to the threshold. For the Baird's tapir population, current genetic diversity is already below the 90% threshold (Table 2-2). Norton and Ashley [2004] found high levels of allelic diversity for North American captive Baird's tapirs, despite the few number of founders, but found evidence of increased divergence from wild populations. Increasing current genetic diversity, while minimizing inbreeding and loss of genetic diversity, can greatly lengthen the time to the 90% viability risk threshold [Earnhardt et al., 2001]. This will require: (1) new founders into the North American captive populations through exchanges with zoos in other regions (e.g., Central America as suggested by Norton and Ashley [2004]) and (2) transfers of individuals within the population to actively manage reproduction in order to equalize ecological fitness among individuals and maintain genetic diversity.

Fortunately, tapirs do not appear to be negatively affected by transfers between zoos. In fact, a positive relationship was found between longevity and number of transfers. This, however, may be an artifact of life span, with longer lives allowing more opportunities for transfers between zoos. Thus, the likelihood of being transferred to another zoo increases with age. While individual reproduction was not correlated with number of transfers, birth rate at zoos tended to increase with transfer rate. This potentially reflects the reproductive management of tapirs, with zoos transferring in individuals for mating and transferring out young from successful matings. In fact, reproductive rate was highly positively correlated with the number of transfers of individuals out per year (Spearman's Rho = 0.6239, $P < 0.01$).

Reproductive rate at zoos also was positively correlated with number of enclosures and complexity. As number of enclosures increases, the total enclosure area increases providing more space available to individuals. Carlstead et al. [1999] found a positive correlation between total enclosure area and number of births at a zoo for black rhinos. Not surprisingly, zoos with more enclosures also tended to house more tapirs (Spearman's Rho = 0.4152, $P < 0.01$). Consequently, zoos with more females that are currently living had a higher reproductive rate (Spearman's Rho = 0.4152, $P < 0.01$).

In addition to the number of living tapir females, the level of enclosure complexity may influence reproductive rate. While no single complexity component was strongly correlated with tapir reproduction, greater complexity in terms of the total combination of topography and the number of trees, shrubs, shelters, mud wallows, and pools helped further explain the variance in reproductive rates. Similarly, Miller-Schroeder and Paterson [1989] concluded that larger, more complex enclosures increased the likelihood of successful reproduction for captive gorillas (*Gorilla gorilla*). While complexity tends to be a qualitative rather than quantitative variable, it generally refers to the number and variety of features in the environment. Cage area/volume, provisions for vertical cage use, such as ladders or ropes, live vegetation, and nesting material were all factors associated with gorilla reproduction [Miller-Schroeder and Paterson, 1989]. In this study, I used a relative measure of complexity using topography and number of enclosure attributes for comparisons among zoos and found a positive relationship between the complexity index and reproductive rate. However, since complexity was correlated with main exhibit size, it is uncertain whether complexity alone, without concurrent increases in enclosure size, would affect tapir reproduction. Both factors may play a role in reproductive success.

Mortality of tapirs was associated with health problems, but enclosure size, complexity, disturbances, or climate were not useful predictors. Survivorship for larger, long-lived species typically follows a type I curve, with the majority of mortality occurring in older age classes [Pearl and Miner, 1935; Gotelli, 1995]. The survivorship curves for North American captive tapirs, however, appear to be closer to a type II or III, with mortality increasing in the younger age classes and nearly equal proportions in the remaining age classes (Fig. 2-3). Approximately one fifth of tapir mortality occurred within the first 30 days of life. Thus, mean life expectancy is much lower than the maximum longevity of 36 years. Monitoring and analyzing juvenile mortality would be profitable, especially because inbreeding depression can result in reduced survivorship and fecundity [Falconer, 1981; Frankel and Soule, 1981; Ralls and Ballou, 1983].

Percent public perimeter, density, and percent variation between enclosure areas were useful predictors of health. Interestingly, as public perimeter increased, the frequency of health problems decreased. The percent public perimeter was not strongly correlated with enclosure area nor any other measured descriptive variable, including position of the public relative to the animals (i.e., same level, higher, or lower). Number of transfers per year and percent public perimeter were both classified as disturbance variables, with the prediction that disturbances may lower reproductive success and health. However, these research findings support the assertion by Shoemaker et al. [2003] that tapir species are not particularly sensitive to stimuli outside their enclosures. Indeed, Thompson [1989] found that ungulates in their extra large size class, of which tapirs would qualify, were less vigilant towards the public. Alternatively, the public may serve as a form of positive stimulation for tapirs. Captive environments can be stimulus impoverished, leading to various negative behavioral changes [Carlstead, 1996]. If public presence was acting to reduce boredom, then the probability of stereotypic behaviors might be lower in zoos that had a greater percent public perimeter. This, however, was not found to be the case ($G^2 = 0.34$, 1 df, $P = 0.56$). It is also possible that percent public perimeter is positively correlated with distance from enclosure edge or spacing of people along the perimeter, decreasing the impact of public presence. Unfortunately, neither of these variables were measured to test these hypotheses.

As predicted, health problems did tend to increase with increasing density. Recommended outdoor enclosure size is 55.74 m^2 per animal [Shoemaker et al., 2003] with a minimum of at least 18.58 m^2 per animal [Barongi, 1997, 2003]. The minimum outdoor enclosure requirement would result in a density of 54 individuals/1000 m^2 that is much higher than that observed in this study (Table 2-4) and considerably higher when compared to maximum densities in the wild of 0.001 individuals/1000 m^2. Increased densities levels could affect tapir behavior and disease transmission. Clubb and Mason [2003] found a positive relationship between home range size and stereotypic pacing for 35 different species of carnivores. Stereotypic behavior may become well-developed for some tapirs even after they have been moved among several larger exhibits, as found in a study examining the effects of activity-based exhibition of Malay tapirs and four other captive mammals [White et al., 2003]. While infectious diseases only accounted for one-third of captive tapir mortalities, respiratory diseases were identified as an important cause of death across age classes [Janssen et al., 1996]. Disease transmission rates are typically density-dependent, with the risk of infection increasing with population density [Anderson and May, 1981].

Furthermore, a negative correlation between health problems and the variation between enclosure areas exists. Larger outdoor exhibit sizes coupled with indoor quarters and/or outdoor holding areas may be important for minimizing health problems. Indoor quarters and outdoor holding areas are recommended to be 16.72 and 37.16 m^2 in size [Shoemaker et al., 2003]. Using the recommended enclosure sizes, the coefficient of variation of enclosure area would be 53.41%. This is lower than the observed variation in enclosure area (Table 2-4). Thus, tapir health may benefit from increasing outdoor enclosure sizes, which would reduce density and increase the variation in area.

Climate also seemed to play a role in specific health problems, such as foot and eye problems. Zoos in warmer, wetter climates with larger, more complex enclosures experienced fewer foot problems. Zoos in colder climates need to keep tapirs indoors for longer periods, where they are subject to harder, concrete surfaces. These harder surfaces tend to lead to foot abrasions and lameness [Janssen et al., 1996; Shoemaker et al., 2003]. Thus, climate serves in part as a surrogate to time on harder surfaces. Climate was also important for eye health, particularly for Malay tapirs. Zoos in warmer climates experienced more eye problems, indicating that shade may not be sufficient for these forest-dwelling species.

While rectal prolapse was historically a major problem for captive tapirs [Barongi, 1993], the incidence was reported to be rare and occurred in only 2% of the zoos surveyed. Consequently, the conditions associated with the incidence of rectal prolapse could not be adequately examined. However, pools were thought to be an important factor for preventing rectal prolapse [Barongi, 1993, 1997, 2003; Shoemaker et al., 2003], and it should be noted that all zoos in this research had at least one pool in a main exhibit. Despite the improvement in rectal prolapse health, skin problems still appear to be a health concern for tapirs. An acute vesicular skin disease of unknown etiology that results in skin lesions and occasionally rear limb weakness has been documented for tapirs in several zoos [Finnegan et al., 1993; Barongi, 1993, 2003; Shoemaker et al., 2003]. The presence of mud wallows may help improve skin health, particularly for South American and Malay tapirs which showed a higher frequency of skin problems. In the wild, tapirs are known to use wallowing holes, in addition to lakes and rivers [Padilla and Dowler, 1994; Foerster and Vaughan, 2002]. Mud wallows can serve several different functions for animals, including social behavior, thermoregulation, grooming, and reducing ectoparasites, biting insects, and skin irritations [Fouraker and Wagener, 1996; McMillan et al., 2000]. However, mud wallows can be a reservoir for disease pathogens (e.g., leptospirosis [Neiffer et al., 2001]), so proper maintenance and sanitary conditions are advised.

These research findings provide empirical evidence that substantiate the AZA husbandry standards [Shoemaker et al., 2003] for the variables measured in this study. Given that Malay, South American, and Baird's tapirs have similar life history traits, with no apparent differences in disease patterns [Janssen et al., 1996] or behavior [Barongi, 1993], similar management appears appropriate. Exceptions include increased shade requirements for Malay tapirs in zoos in hotter climates and current breeding restrictions for the phase-out population of South American tapirs. Increases in enclosure size and complexity could provide increases in breeding success for an institution and improvement in health of tapirs. However, considering space restrictions in zoos, complexity may be easier to manipulate, by adding various attributes such as trees, shrubs, pools, mud wallows, and topographic relief to exhibits. Increasing complexity over its range would potentially yield an increase of nearly 1 birth per female over 10 years, with the odds of successful reproduction 14 times more likely. Foot problems also may occur less frequently in more complex exhibits. Furthermore, increasing the amount of exhibit edge exposed to the public may confer health benefits for unknown reasons and should be further examined. Tapirs are known to have considerable individual variation in behavior [Barongi, 1993, 1997, 2003; Shoemaker et al., 2003], which could influence specific responses to environmental variables. Behavioral research, akin to the Methods of Behavioral Assessment Project [Carlstead, 1999], may be useful to account for this individual variation and to monitor behavioral changes in relation to husbandry practices.

CONCLUSIONS

1. The captive tapir populations in North America are relatively small, requiring new founders and intensive genetic management for maintaining genetic diversity. This is particularly critical for the Baird's tapir, since genetic diversity is already below the 90% viability risk threshold. Currently the captive tapir populations have an even sex and age distribution, with zero population growth. Although increases in population size

to the target of 75 individuals for the Baird's and Malay tapirs will help reduce demographic stochasticity, the founder effect will still be considerable. Inbreeding depression will likely increase without new individuals brought into the North American captive populations.

2. Both area and complexity may play a role in reproduction and health of tapirs in captivity. Zoos with larger enclosure variation and lower tapir density tend to have fewer health problems. Reproduction also increased with the number of enclosures and the complexity of the enclosures.

3. In addition to pools, mud wallows may reduce the frequency of skin problems in tapirs. The incidence of rectal prolapse has been greatly reduced, possibly due to the current establishment of pools in tapir enclosures.

4. Additional research is needed to further examine the correlations identified. A correlation between eye health and climate was found, indicating that the percent shade was still insufficient for Malay tapirs in warmer climate zoos. However, the amount of shade that is sufficient to reduce eye problems still needs to be identified. In addition, factors influencing individual reproduction and infant mortality should be investigated, especially in relation to inbreeding. Constructing individual behavioral profiles may facilitate reproduction management and husbandry of captive tapirs.

5. In general, these research findings support the AZA husbandry recommendations for managing tapirs in captivity.

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Table 2-1. Eigenvectors for the first two principal components of the climate principal components analysis.

Climate Variables	Principal Component 1 (w1)	Principal Component 2 (w2)
Days ≤ 32 F	- 0.54857	0.03575
Days ≥ 90 F	0.37252	0.56921
Mean annual temperature	0.55149	0.12651
SD temperature	- 0.46820	0.24190
Precipitation	0.19225	- 0.77473
Percent Variance Explained	61.46%	19.83%

Table 2-2. Summary demographics of captive tapir populations in North America.

	Baird's	South American*	Malay	All†
Current captive population size	34 (22 ♂, 12 ♀)	40 (23 ♂, 17 ♀)	52 (23 ♂, 29 ♀)	125 (65 ♂, 58 ♀)
Number of founders	8	17	30	55
Population growth rate	1.00	1.00	0.99	1.00
Current genetic diversity	0.86	0.90	0.96	0.91
Mean Inbreeding	0.031	0.015	0.001	0.016
Mean / Median age at first birth (years)	5.3 / 4 (σ=3.7; n=17 ♀)	5.8 / 4 (σ=2.7; n=86 ♀)	5.6 / 5 (σ=1.8; n=50 ♀)	5.6 / 4.3 (σ=1.8; n=116 ♀)
Range of age at first birth (years)	2.2-12	1.7-14	2.8-11.1	1.7-14
Mean / Median birth interval (days)	744 / 722 (σ=175; n=16 ♀)	709 / 637 (σ=395; n=62 ♀)	749 / 736 (σ=153; n=38 ♀)	727 / 679 (σ=308; n=116 ♀)
Mean number of offspring	4.9 (σ=3.0; n=33)	3.6 (σ=2.8; n=163)	3.8 (σ=2.6; n=85)	3.8 (σ=2.8; n=281)
Percent mortality for < 30 days old	16% (n=85)	24% (n=297)	18% (n=176)	21% (n=558)
Percent mortality for < 1 year old	20% (n=85)	30% (n=297)	26% (n=176)	27% (n=558)
Longevity (years)	22 ♂, 27 ♀	36 ♂, 30 ♀	36 ♂, 31 ♀	36 ♂, 31 ♀

* South American tapir is currently designated as a Phase-Out Population, defined as "currently in AZA institutions but should be phased out through a monitored breeding moratorium" [AZA Tapir TAG, 2004].

† Excluding mountain tapir; no studbook established for current population of 6 individuals in North America.

Table 2-3. Summary of mean tapir reproductive rate, mortality rate, and weighted frequency of health problems for zoological institutions in North America.

	Baird's	South American	Malay	Mountain	All
N (zoos)	13	14	22	4	53
Reproduction	0.0568 (σ = 0.0704)	0.0477 (σ = 0.0389)	0.0567 (σ = 0.0717)	*	0.0540 (σ = 0.0620)
Mortality	0.0153 (σ = 0.0306)	0.0136 (σ = 0.0145)	0.0192 (σ = 0.0353)	*	0.0166 (σ = 0.0291)
Health Problems	3.1 (σ = 2.2)	3.7 (σ = 2.7)	5.0 (σ = 2.4)	3.0 (σ = 3.6)	4.1 (σ = 2.6)

* No studbook data

Table 2-4. Summary statistics for model variables.

Variables	Model	N	Mean	Median	SD	Range
Number of enclosures	N	53	3.9	4.0	1.8	1-9
CV Area of enclosures	Acv	50	120.3	126.9	24.5	62.1-161.4
Mean main exhibit area (m^2)		53	3587.7	358.0	13505.6	70-92900
Density (# individuals/1000 m^2)	D	45	5.13	3.08	6.91	0.03-43.06
Complexity Index	C	53	5.0	5.0	1.36	2-8
% Perimeter with public access	P	51	32.5	26.4	20.9	0-100
Number of transfers per year	T	49	0.47	0.42	0.27	0.07-1.33

Table 2-5. Top five regression models and their associated Akaike weights (w_i). The regressions models included number of enclosures (N), density (D), coefficient of variation of area (Acv), complexity index (C), number of transfers per year (T), percent public access along enclosure perimeter (P), and climate principal components (w1 and w2). K is the number of parameters in the model, AICc is Akaike's information criterion corrected for small sample size, and Δ is the difference between the selected model from the best model in the set.

Models	K	AICc	Δ	w_i
Reproduction:				
N C T	5	-247.37309	0	0.13849
N T	4	-247.18563	0.18746	0.12610
T	3	-246.74403	0.62907	0.10112
C T	4	-246.62691	0.74619	0.09537
D C T	5	-245.16011	2.21298	0.04580
Mortality:				
0 (Intercept)	2	-306.94728	0	0.10873
Acv	3	-306.58895	0.35833	0.09090
w2	3	-305.11282	1.83446	0.04345
Acv C	4	-305.11191	1.83537	0.04343
D	3	-304.94445	2.00283	0.03994
Health Problems:				
D P	4	70.24052	0	0.23128
Av P	4	70.90332	0.66280	0.16604
D P T	5	72.57838	2.33785	0.07186
Av C P	5	72.70264	2.46212	0.06753
P	3	72.73909	2.49856	0.06631

Table 2-6. Relative importance of the explanatory variables in the multiple regression models for reproduction and health problems. Rankings were based on the sum of the Akaike weights (w_i) across models that contain each variable divided by the number of models in the set (M).

	Reproduction		Health Problems	
Variables	$\sum w_i / M$	Ranking	$\sum w_i / M$	Ranking
T	0.028509	1	0.007539	4
N	0.017128	2	0.002313	4
C	0.012234	3	0.007344	4
P	0.007527	4	0.029116	1
D	0.006664	4	0.017933	2
Acv	0.004574	4	0.014495	3
w1	0.004923	4	0.004302	4
w2	0.001288	4	0.001120	4

Table 2-7. Health problems by category for each tapir species, ranked by occurrence at zoological institutions in North America. Rare is defined as occurring infrequently in any individual; common is occurring multiple times for one individual or occurring in several individuals. The remaining percentages for each health problem reflects no occurrences.

Health Problems	Baird's	So. American	Malay	Mountain	All
	% (n = 13)	% (n = 14)	% (n = 22)	% (n = 3)	% (n = 52)
Skin					
Rare	46	64	55	0	52
Common	0	14	27	67	19
Foot					
Rare	31	21	38	33	31
Common	15	21	24	33	22
Eye					
Rare	15	36	14	33	22
Common	23	7	52	0	29
Oral					
Rare	31	29	36	33	33
Common	8	14	5	0	8
Stereotypic Behavior					
Rare	23	14	43	0	27
Common	0	0	0	0	0
Diarrhea/Vomiting					
Rare	15	7	29	33	20
Common	7	0	0	0	2
Parasitic Infections					
Rare	0	21	24	33	18
Common	0	0	0	0	0
Respiratory					
Rare	15	14	18	0	15
Common	0	0	0	0	0
Colic					
Rare	8	0	14	33	10
Common	0	0	0	0	0
Hemolytic Anemia					
Rare	0	7	5	0	4
Common	8	0	0	0	2
Rectal Prolapse					
Rare	0	7	0	0	2
Common	0	0	0	0	0
Vasculopathies					
Rare	0	7	0	0	2
Common	0	0	0	0	0

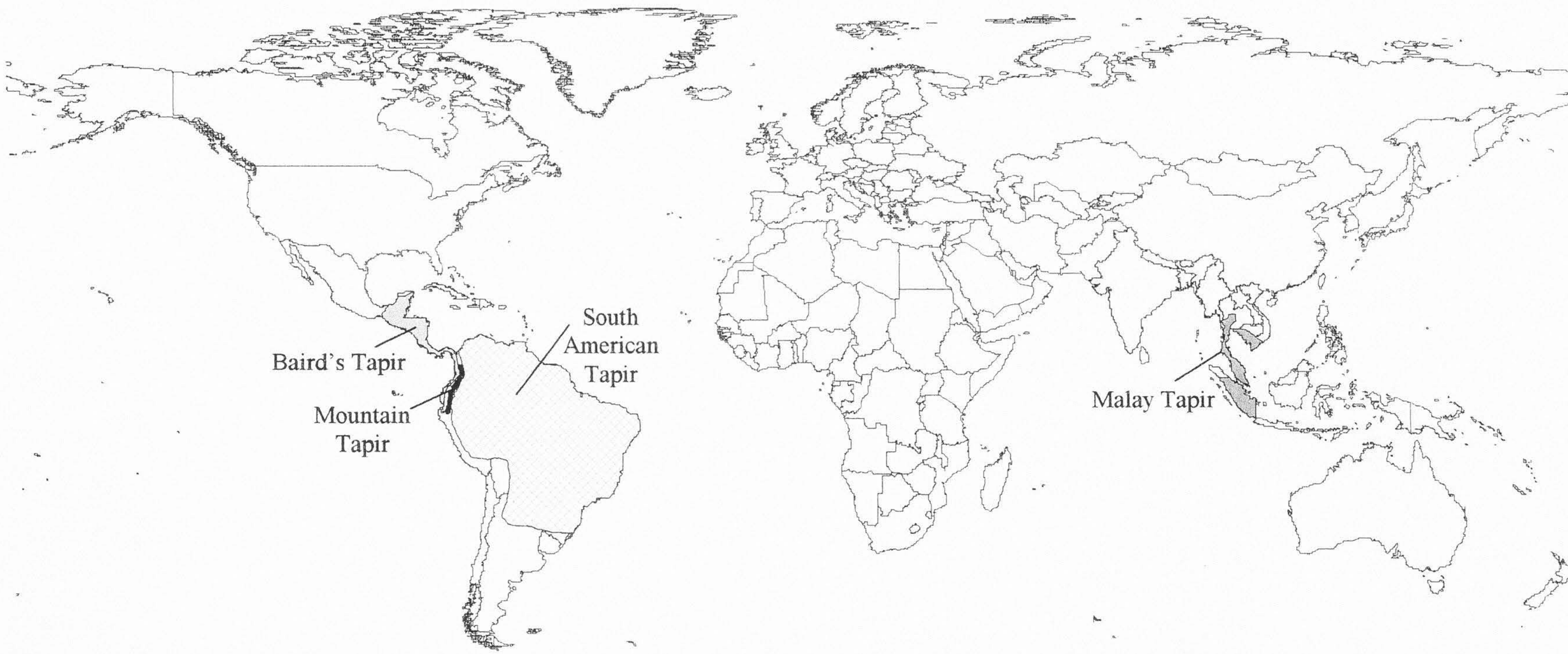

Fig. 2-1. Distribution map of Tapirus spp. (adapted from Brooks et al., 1997). Shaded regions represent extent of distribution; actual distribution is highly fragmented within these regions.

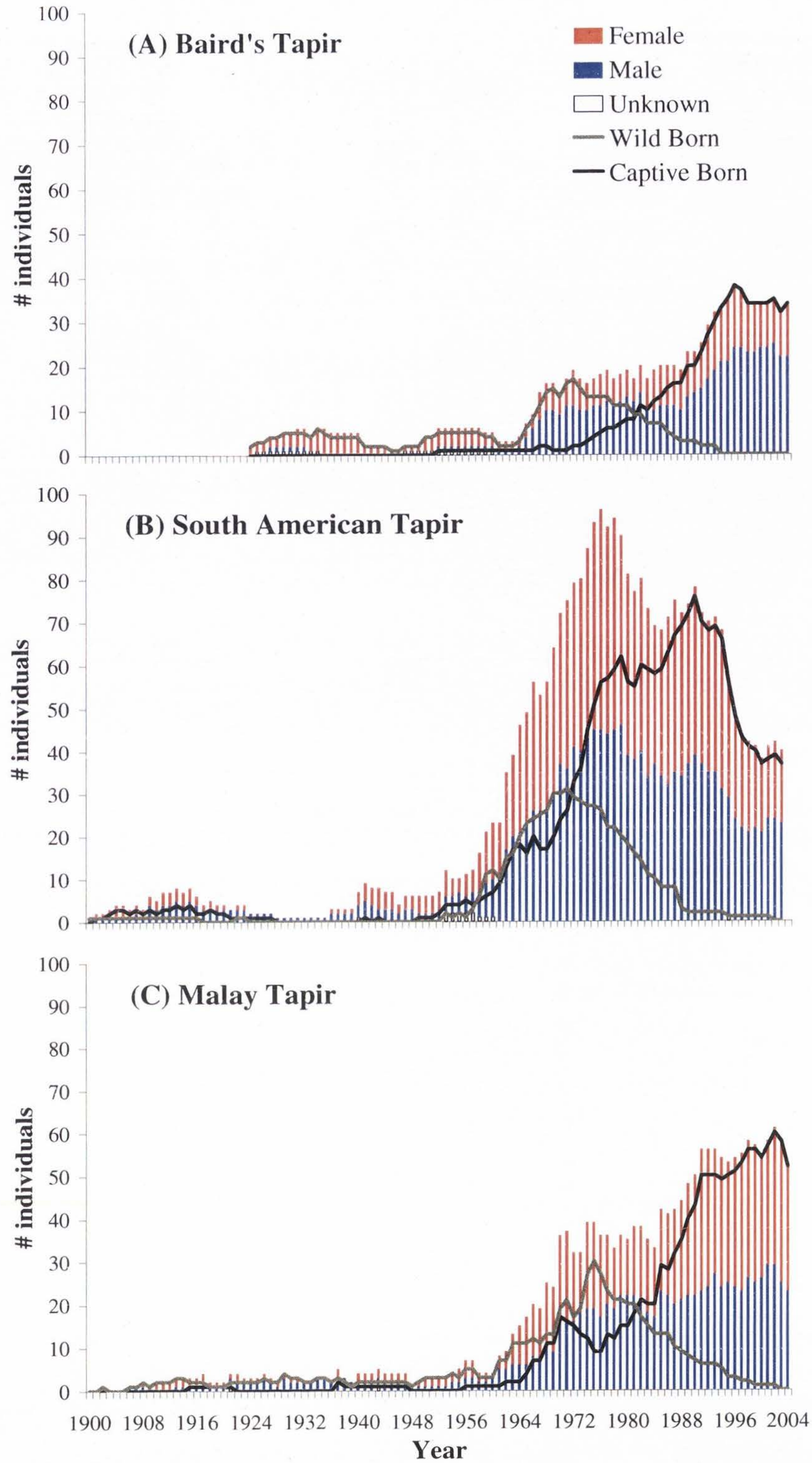

Fig. 2-2. North American captive population trends for (A) Baird's, (B) South American, and (C) Malay tapirs from years 1900 to 2004.

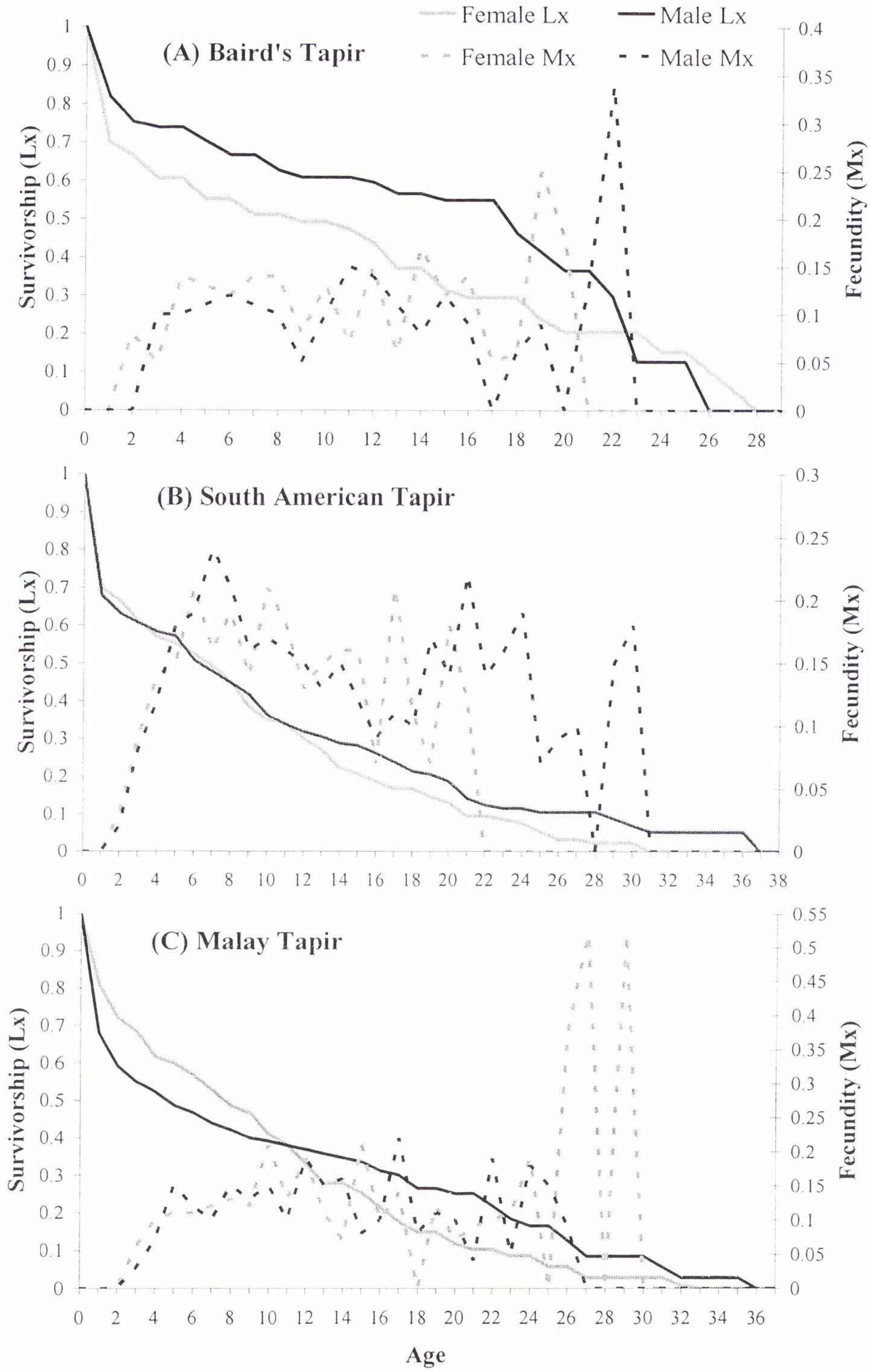

Fig. 2-3. Survivorship and fecundity for (A) Baird's, (B) South American, and (C) Malay tapirs.

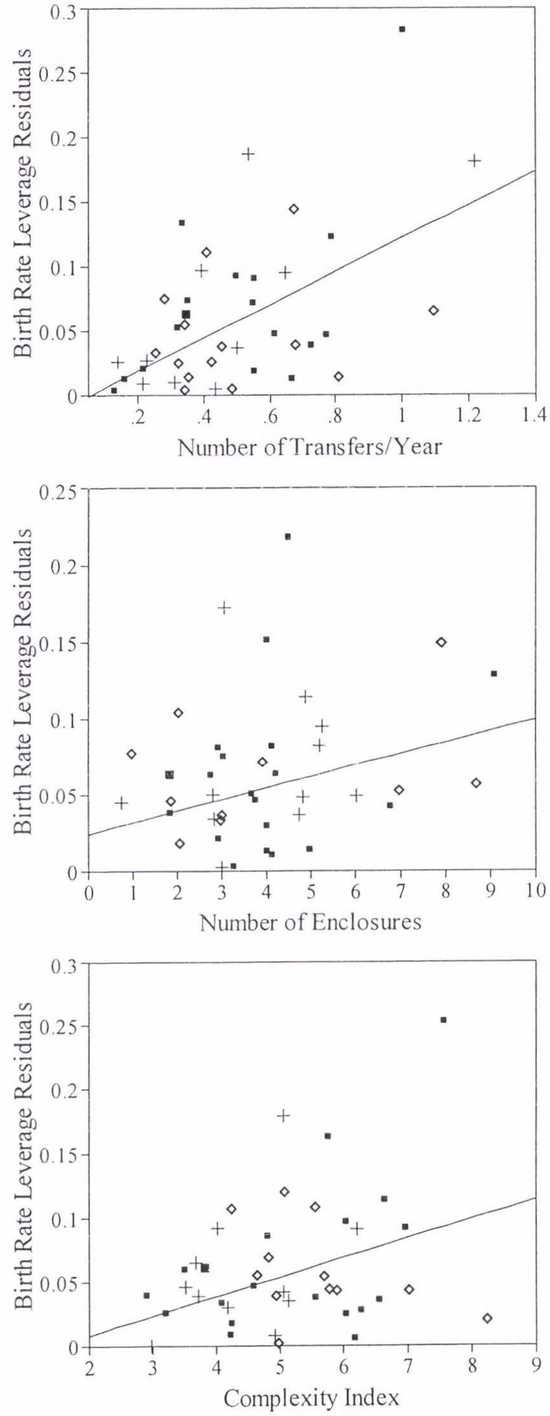

Fig. 2-4. Partial regression plots for number of transfers per year (T), number of enclosures (N), and complexity index (C) in the reproduction regression model ($Y = \beta_0 + 0.1288T + 0.0075N + 0.0152C$; $R^2 = 0.34$). Symbols indicate tapir species: + Baird's, ◇ South American, ■ Malay tapirs.

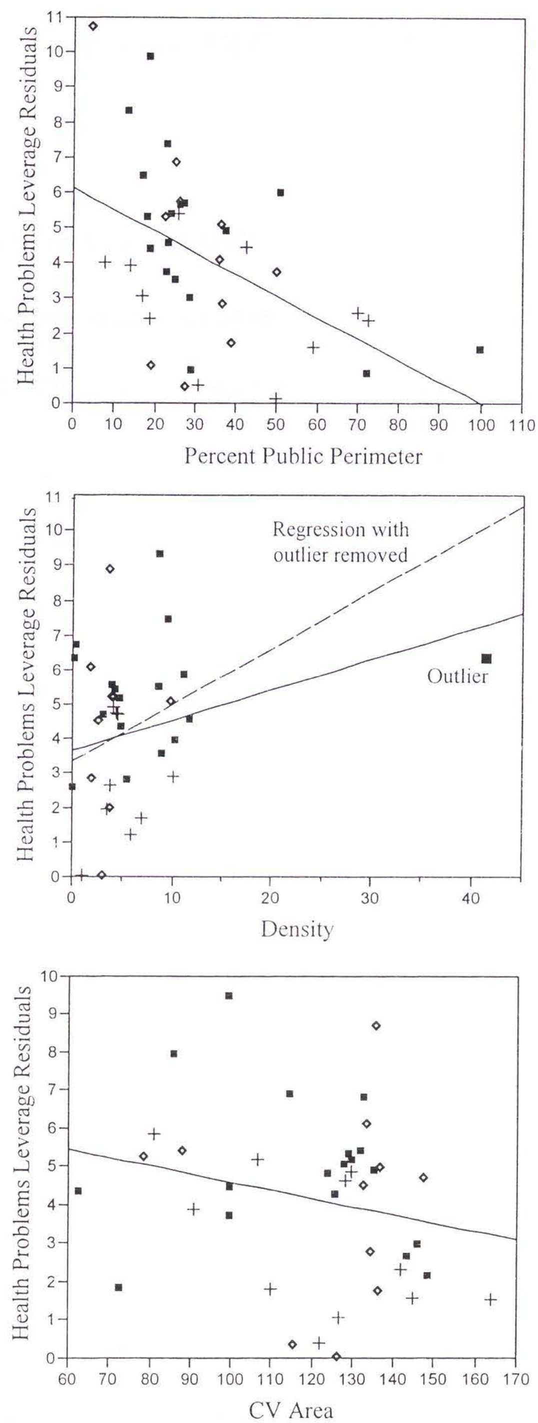

Fig. 2-5. Partial regression plots for the percent of public access along enclosure perimeter (P), number of individuals per 1000 m^2 (D), and coefficient of variation in area (Acv) in the health problems regression model ($Y = \beta_0 - 0.0610P + 0.0881D - 0.0225Acv$; $R^2 = 0.34$). Symbols indicate tapir species: + Baird's, ◆ South American, ▪ Malay tapirs.

CHAPTER 3

RHINOS IN CAPTIVITY

INTRODUCTION

Among the largest terrestrial mammals, rhinos are threatened with the risk of extinction. Ex situ conservation measures have been established for four of the five extant rhino species: black (*Diceros bicornis*), white (*Ceratotherium simum*), Indian (*Rhinoceros unicornis*), and Sumatran (*Dicerorhinus sumatrensis*). The rarest rhino species, the Javan rhino (*Rhinoceros sondaicus*), is not currently held in captivity and only four Sumatran rhinos occur in captivity in North America [Foose, 2005]. Much is known about rhinos as evidenced by the extensive bibliography containing over 8500 publications, compiled by the Rhino Resource Center [Rookmaaker, 2003]. Unfortunately captive management of rhinos is still a challenge. Current problems include high mortality of black rhinos, problems with reproduction for white rhinos, and the foot health problems of Indian rhinos [AZA Rhino Advisory Group, 2002]. One of the goals of the American Zoo and Aquarium (AZA) Species Survival Plan (SSP) Rhino Masterplan is "improvement of captive husbandry and management through research in health, nutrition, behavior, and reproduction to facilitate development of viable populations *ex situ* and to transfer results as appropriate to intensively managed populations *in situ*" [AZA Rhino Advisory Group, 2002]. Although highly complex, examining the individual factors that comprise the captive environment is essential to achieve this goal.

Despite some physical similarities, each rhino species is unique in its distribution, ecological requirements, and social behavior. The Indian rhino occurs in the grassy floodplains in northern India and the Chitawan Valley in Nepal [Laurie et al., 1983; Fouraker and Wagener, 1996], whereas both the black and white rhinos are African species (Fig. 1). The black and white rhinos differ in their habitat preferences, with white rhinos occupying mainly savannahs and black rhinos occupying a range of scrubland and savannah woodland habitat types [Groves, 1972; Hillman-Smith and Groves, 1994; Fouraker and Wagener, 1996]. Indian and white rhinos are primarily grazers, though Indian rhinos are recorded consuming fruit and browse as a small portion of their diet [Groves, 1972; Laurie et al., 1983; Fouraker and Wagener, 1996]. Conversely, black rhinos are mainly browsers, foraging on leaves, twigs, and forbs [Hillman-Smith and Groves, 1994; Fouraker and Wagener, 1996]. Indian and white rhinos are also larger in size than black rhinos, ranging from 1,800 to 2,200 kg compared to 800 to 1,350 kg for black rhinos [Fouraker and Wagener, 1996]. The social structure of these rhino species varies from mainly solitary to semi-social. Black and Indian rhinos are usually solitary, although females and subadults may form temporary associations [Laurie et al., 1983; Hillman-Smith and Groves, 1994; Fouraker and Wagener, 1996]. Being possibly less solitary than the Indian rhino, black rhinos may have overlapping home ranges [Fouraker and Wagener, 1996]. White rhinos are semi-social, with females and subadults commonly in groups and males usually solitary [Groves, 1972; Owen-Smith, 1974; Fouraker and Wagener, 1996].

Understanding the ecological and behavioral differences between each of the rhino species is important for determining adequate conditions in captivity. An AZA Rhinoceros Husbandry Resource Manual [Fouraker and Wagener, 1996] was developed to provide guidelines for the optimal management of captive rhinos. The recommended minimum grouping size for breeding is at least one male and two or more females for white rhinos, one breeding pair for black rhinos, and one breeding pair held separate until peak estrus or held together in large exhibits for Indian rhinos. Enclosure design for breeding is recommended to include an outdoor enclosure that is ~2,322 m^2 in size for black rhinos and ~2,787 m^2 in size for white and Indian rhinos. The minimum outdoor area per individual rhino is stipulated as 139 m^2 [Fouraker, 1997]. Fouraker and Wagener [1996] suggest that rhinos be kept mainly outdoors within temperature constraints, but that indoor housing be provided particularly for zoos in colder climates. Other recommended enclosure attributes include the presence of pools, mud wallows, visual barriers such as trees, logs, or dirt mounds, shade shelters, and scratching posts.

The purpose of this research is to identify the factors associated with captive rhino reproduction, mortality, and health problems. Previous studies have indicated a number of variables that may influence successful husbandry, including the number of individuals, enclosure size, climate, solid walls surrounding the enclosure, public access around the exhibit perimeter, response to keepers, pools, mud wallows, soft substrates, overall enclosure complexity, diet, and vaccinations. For example, Carlstead et al. [1999a] found that zoos with a single black rhino female had higher reproductive rates than zoos with multiple females. Lindemann [1982 in Emslie and Brooks, 1999], however, found that white rhino reproduction was significantly higher when zoos had multiple males.

Rhinos are generally known to have large space requirements for breeding due to their physical size and aggressive courtship behavior. White rhino reproduction has been observed to be successful in large enclosures with large group sizes [Emslie and Brooks, 1999]. A positive relationship between reproduction and enclosure size also was identified for black rhinos [Carlstead et al., 1999a]. Similarly for Indian rhinos, Lang [1975] attributed lack of reproduction at several zoos to inadequate space.

Climate also may affect reproduction, health, and activity patterns of rhinos. Kretzschmar et al. [2004] found that free-ranging adult male white rhinos had higher testicular activity, measured by androgen metabolite concentrations, during the rainy season. Ambient temperature and percent sunshine can influence peaks in activity, with feeding and resting periods being altered [O'Connor, 1986]. Moreover, climate may indirectly cause differences in reproduction rates through differences in husbandry practices, because zoos in colder climates keep rhinos indoors during cold periods for protection [Rawlins in O'Connor, 1986].

Other indirect effects of climate are related to additional correlations with husbandry or enclosure variables. Carlstead et al. [1999a, b] found that zoos in colder climates had a higher percentage of solid enclosure walls, which were correlated with behaviors negatively associated with black rhino female reproductive success. Another example includes foot problems of Indian rhinos, which may be more prevalent in colder climate zoos because of the time spent indoors on hard, abrasive surfaces [von Houwald, 2001].

The percentage of enclosure perimeter that the public could access was found to be positively correlated with black rhino mortality [Carlstead et al., 1999a], and higher stress levels among black rhino individuals, measured by mean corticoid concentration [Carlstead and Brown, 2005]. O'Connor [1986] speculated that public proximity may influence white rhino activity patterns, though no apparent behavioral changes were observed. Reactions to keepers also may be important. White rhino stress levels may differ depending on the degree to which an individual behaves friendly towards keepers, with individuals that are "friendlier" having lower mean stress hormone concentrations [Carlstead and Brown, 2005]. In a study of several different species of ungulates, Thompson [1989] found higher vigilance and less time eating and drinking while the keeper was within the enclosure.

Hediger [1950] was among the first to emphasize the importance of quality over quantity of space. Mud wallows and pools are two critical elements for rhino enclosure design. Wallowing in mud is a common activity among rhinos [Groves, 1972; Laurie et al., 1983; Fouraker and Wagener, 1996] and helps to regulate temperature and maintain skin health by reducing ectoparasites, biting insects, and skin irritations [Laurie et al., 1983; Fouraker and Wagener, 1996; McMillan et al., 2000]. Access to pools is particularly important for Indian rhinos, who can spend up to 70% of the day feeding or resting in lakes and rivers in the wild [Laurie in von Houwald, 2001]. Substrate and topography are other features which may influence rhinos. Abrasive surfaces, such as concrete or gravel, are considered to be the primary cause for Indian rhino foot problems [von Houwald, 2001]. Carlstead et al. [1999a] also suggest that visual barriers or topographic relief may offset total enclosure size. All of these factors combined create the total enclosure complexity.

Diets of captive rhinos are recommended to follow the equine nutritional model [Fouraker and Wagener, 1996; Oftedal et al., 1996; Fouraker, 1997], but this regime may be inadequate for providing the specific nutritional needs of rhinos [Fouraker and Wagener, 1996]. The diet of rhinos has been implicated in various health problems [Fouraker and Wagener, 1996] and as a cause for poor captive reproductive rates in black rhinos [Emslie and Brooks, 1999]. Diet also may be a cause of foot problems for Indian rhinos by potentially lacking in essential nutrients, such as biotin, or by attributing to increased weight [von Houwald, 2001].

The health of rhinos varies between species, with the black rhino known to be plagued with the most disease syndromes [Fouraker and Wagener, 1996]. Skin problems, colic, and infectious diseases, such as tuberculosis and encephalomyocarditis, can affect all species of rhinos. Indian rhinos have had a high incidence of chronic foot problems [von Houwald, 2001]. Black rhinos, however, appear to be more susceptible to diseases of unknown etiology [Fouraker and Wagener, 1996; Fouraker, 1997]. A major cause of death for black rhinos has been hemolytic anemia, which may be associated with *Leptospirosis interrogans* infection, exposure to chemical compounds, diet, or a number of other stressors [Miller et al., 1987; Fouraker and Wagener, 1996]. Vaccinations against leptospiral bacteria, particularly for black rhinos, are recommended [Fouraker and

Wagener, 1996; Fouraker, 1997]. Other vaccinations include tetanus, rabies, encephalitis, and West Nile virus.

Each of these factors will be examined to describe the captive environment experienced by rhino species in North America. I constructed models to better understand the relationships and interactions between variables by relating husbandry and enclosure variables to reproduction, mortality, and health. Since reproduction and health are inadequately known for rhinos [Fouraker and Wagener, 1996], these descriptive models for each rhino species may help elucidate the patterns important for their successful captive management.

METHODS

Black, white, and Indian rhinos were included in this study. North American Regional Rhino studbooks [Foose, 2005] were used to calculate reproduction and mortality for each species. Institutional summary reports were created using the Single Population Analysis and Records Keeping System (SPARKS) [ISIS, 2004].

In addition, I conducted a census of all North American zoos housing rhinos. Using the International Species Information System (ISIS) Species Holdings [ISIS, 2003], I identified institutions in the United States and Canada currently housing rhinos. In 2003, I mailed a survey instrument to these zoological institutions to gather information on enclosure attributes and management practices. The American Zoo and Aquarium Association (AZA) Rhino Advisory Group approved this survey [Blumer, pers. comm.] and a letter of support was included with the survey forms. Over 90% response rate was achieved. Variables used in analyses that were included on the survey were: main outdoor enclosure area, indoor enclosure area, percent of public access along enclosure perimeter, percentage of enclosure perimeter that obstructed an animal's view (i.e., % walls), enclosure substrate, topography, percent shade, amount of vegetation, number of water pools and mud wallows, diet, number of feedings per day, time spent per day by keepers, vaccinations, and frequency of health problems.

Climate for each zoo was determined using climatic data from the National Climatic Data Center [2004] and Utah Climate Center [2005]. I used the nearest weather stations to each institution to obtain data on the mean number of days with a minimum temperature of 32° F or lower, mean number of days with a maximum temperature of 90° F or higher, mean annual temperature, standard deviation of normal daily mean temperature, and the mean normal precipitation, including the liquid water equivalent of snowfall. Because these climatic variables were highly intercorrelated, a principal components analysis was used to summarize climate. The first two principal components for climate described 81% of the variation (Table 3-1). The first component (Climate Prin1) was characterized by lower mean annual temperature and more days below freezing. The second component (Climate Prin2) was primarily a moisture variable, with increasing precipitation and days above 90° F. Fig. 3-2 shows a comparison of Climate Prin 1 and Climate Prin 2 values for each of the climatic variables.

Area per individual, as a measure of density, was calculated by dividing the total main exhibit area by the number of living animals at an institution. An index of complexity was generated using the number of attributes within the enclosure and a ranking of topography, with level being ranked lowest and hills highest. Attributes included the presence of trees, shrubs, pools, mud wallows, and shelters. Mortality for each species at an institution was calculated by dividing the total number of deaths by the number of individuals held at the institution and by the total number of years that each species was housed, in order to standardize across institutions:

$$\text{Mortality rate} = \frac{\#\,deaths}{[N(rhinos) \cdot \#\,years]} \qquad \text{(Eq. 1)}$$

Reproductive rate was similarly determined by dividing the total number of births, regardless of survival of the young, by the number of females held at the institution and by the total number of years housed:

$$\text{Reproductive rate} = \frac{\#\,births}{[N(females) \cdot \#\,years]} \qquad \text{(Eq. 2)}$$

Reproduction was calculated only for institutions that held at least one potential breeding pair. Health problems were grouped into the following categories: foot, eye, skin, dental/oral, respiratory diseases, colic, chronic diarrhea or vomiting, hemolytic anemia, parasitic infections, rectal prolapse, vasculopathies, and stereotypic behavior. The overall, combined health at a zoological institution was measured using the occurrences of each health problem, weighted by its frequency rank of common, rare, or no occurrences.

Data analysis was performed using SAS [SAS Institute, 2003] and JMP IN [SAS Institute, 2004]. Due to significant differences among species, each species was analyzed separately. Summary statistics were calculated for each of the explanatory variables and correlations among variables were analyzed. This was primarily an observational and exploratory study, examining the relationships among the response variables (i.e., reproduction, mortality, and frequency of health problems) with the various husbandry and captive environment variables. Because of this, cause and effect relationships cannot be demonstrated, but rather correlations identified that need further examination. Identifying the model that best described the data was the primary objective.

Classification and regression trees (CART) for reproduction, mortality, and health were constructed for each of the rhino species. CART was chosen as an analysis tool because of its ability to deal with non-normally distributed data, correlations among variables, and complex interactions among variables [Breiman et al., 1984; De'ath and Fabricius, 2000; Karels et al., 2004]. As a nonparametric technique, CART splits the data into two groups, increasing the homogeneity within each group. Splits with the largest effect size were chosen. The recursive partitioning of the data was continued until the best fit with the lowest misclassification rate was achieved. A 5-fold cross validation was performed to calculate a cross-validated R^2.

In addition, polytomous ordinal logistic regression was used to examine the most common health problems reported on the zoological survey. Health problems that were further investigated included foot problems for Indian rhinos, hemolytic anemia for black rhinos, and skin problems for all three species of captive rhinos. Hemolytic anemia and white rhino skin problems were analyzed using the presence or absence of these conditions rather than the ranked frequencies due to few common occurrences.

RESULTS

Mean reproduction, mortality, and health differed between rhino species (Table 3-2). Variation among zoos was considerable, but on average, reproductive rate in captivity was highest for black rhinos and the least for white rhinos. White rhinos appeared to have the highest mortality rates, but the mean was strongly influenced by two outliers. Excluding these outliers resulted in a mean mortality rate of 0.0053 ($n = 38$; $\sigma = 0.0068$). Indian rhinos had the lowest mortality rates, but a high frequency of health problems, along with black rhinos. On average, white rhinos had the fewest number of health problems. Although frequency of specific health problems differed, skin problems were universal for all three rhino species, ranking first for black and white rhinos and second for Indian rhinos (Table 3-3). Foot problems were most prevalent for Indian rhinos.

Considerable variation between zoos also existed for the enclosure and husbandry variables used to describe the captive environment (Table 3-4). Density and enclosure areas differed most among rhino species, though the distribution of the data is highly skewed. Using median values for exhibit area, white and Indian rhinos still tended to have larger enclosure areas (1985 m^2 and 1208 m^2, respectively) than black rhinos, with a median exhibit area of 910 m^2.

Despite being based on the equine model, diet varied among zoos for each of the species (Table 3-5). In general, rhinos are fed mainly hay and commercial grain pellets. Black rhinos were fed nearly equal proportions of alfalfa and mixed grass hay, whereas white and Indian rhinos were fed a greater proportion of mixed grass hay. Black rhinos also were fed a greater percentage of browse, though it only comprised a small percentage of their total diet. Overall, more browse and produce was included in the diet for black and Indian rhinos than for white rhinos. In addition, over half the zoos surveyed provided food continuously for Indian rhinos compared to approximately one-third for black and white rhinos (Table 3-4).

Black Rhino

Black rhino birth rates were best explained by climate and mean exhibit area, accounting for nearly three quarters of the total variation ($R^2 = 0.74$; Fig. 3-3a). Zoos in warm, wet climates had the highest birth rates and exhibit sizes < 583 m^2 at zoos in cooler, drier climates had the lowest birth rates. However, a non-linear relationship with exhibit size was found. Exhibit sizes ≥ 583 m^2 yielded a higher birth rate, but exhibit size beyond 1047 m^2 ranked the next lowest for birth rate. The estimated error of this model, determined using 5-fold cross-validation, was minimal with a cross-validated R^2 equal to 0.67.

Mortality was grouped by exhibit area, climate, and exhibit complexity (Fig. 3-3b). The lowest death rates were among zoos with the mean exhibit area < 1115 m^2 and the complexity index ≥ 4.25. Complexity index values at or above this level indicate exhibits with some topographic relief and the presence of three or more enclosure attributes such as trees, shrubs, pools, mud wallows, and shelters. The highest mortality occurred in zoos in warm, wet climates with mean exhibit area ≥ 1115 m^2. This model explained over half of the total variation (51%), with a cross-validated R^2 of 0.46.

Health of black rhinos was best described by the number of males, vaccinations, and mean exhibit area, although only 40% of the variation was explained by this model

(Fig. 3-3c). Health problems were minimized for zoos with less than 2 males and mean exhibit areas ≥ 786 m^2. The highest weighted frequency of health problems occurred in zoos with two or more males and less than two different types of vaccinations. With a cross-validated R^2 of 0.28, however, this model is speculative.

No significant correlations were found when examining black rhino skin health. Hemolytic anemia, however, was associated with total number of individuals and percent of alfalfa in their diet ($G^2 = 8.56$, 2 df, $P = 0.01$). In general, zoos that held only one pair had a lower probability of hemolytic anemia occurring than zoos that held three or more individuals. Increases in alfalfa also showed a positive relationship with hemolytic anemia.

White Rhino

The number of males and total density accounted for 66% of the variation in white rhino birth rates (Fig. 3-4a). The cross-validated R^2 of the model was 0.59. Zoos holding more than two male white rhinos had the highest birth rate. For zoos with less males, density was a critical factor, with higher birth rates in zoos with < 470 m^2 per individual.

Analysis of white rhino mortality was complicated by two zoos with high mortality rates, which heavily influenced model selection. Both these zoos managed white rhinos for less than five years and do not currently hold this species. Including these zoos, no model could be identified that best explained the white rhino mortality data. Consequently these outliers were excluded, leaving 38 zoos that were used for further analysis. Mortality rates were grouped by mean exhibit area, density, and vaccinations ($R^2 = 0.54$; Fig. 3-4b). Among these zoos, the highest mortality rates occurred in zoos with mean exhibit area $\geq 1858\ m^2$ and administered less than 2 different types of vaccinations for diseases. The lowest mortality rates occurred in zoos with mean exhibit area $< 1858\ m^2$ in size, with $\geq 376\ m^2$ per individual. The error rate was small with a cross-validated R^2 of 0.48.

Diet was a major factor for white rhino health. Zoos that provided diets containing ≥ 40% pellets had the highest weighted frequency of health problems (Fig. 3-4c). Diets that were composed of < 40% pellets and contained zero produce had the least health problems. Climate also was a factor, but only contributed 14% of the model sum of squares and explained approximately 6% of the total variation in the data. Both Climate Prin 1 and Climate Prin 2 were weighted equally for variable selection, having the same sum of squares. Interestingly, zoos in warm, dry climates had more health problems. The entire regression tree explained 41% of the total variation, with a cross-validated R^2 of 0.32.

Skin problems were the most frequent problem for white rhinos, but most zoological institutions reported it as a rare occurrence. Analysis of the presence or absence of skin problems indicated that climate, diet, and the time spent by keepers were important factors for white rhino skin health. Climate Prin1 was negatively associated ($G^2 = 3.94$, 1 df, $P = 0.05$), while Climate Prin2 showed a positive relationship with skin health ($G^2 = 6.13$, 1 df, $P = 0.01$). In other words, the probability that white rhinos experienced skin problems was higher for zoos in colder climates, and less for zoos in warmer, wet climates. Moreover, the three zoological institutions that provided an indoor pool did not report any skin problems for white rhinos, although this finding is anecdotal at best. The model that best described skin health, however, was the mean percent produce (i.e., fruit and vegetables) in their diet and the amount of time spent by keepers ($G^2 = 14.38$, 2 df, $P < 0.01$). As these variables increase, so did the probability of skin problems.

Indian Rhino

Indian rhino birth rates were best split between feeding categories. Zoos that continuously fed their rhinos had nearly ten times the birth rate of zoos that fed their rhinos one to two times per day (Fig. 3-5a). This husbandry variable explained approximately 46% of the variation ($R^2 = 0.46$). Due to the small dataset (n=13), 5-fold cross-validation was not performed.

Another husbandry variable, average time spent by keepers per day, was associated with mortality for Indian rhinos. Zoo exhibits that required < 5 hours per day had a lower mean mortality rate than zoos with an average keeper time of ≥ 5 hours per day (Fig. 3-5b). Keeper time was significantly correlated with climate (Climate Prin2), with less time spent in zoos in warm, wet climates (Spearman's Rho = -0.6727, $P < 0.01$). Nevertheless, keeper time better explained the data with an R^2 of 0.57, compared to 0.37 for Climate Prin2.

Climate, however, did explain differences in health. Climate Prin2 explained approximately 31% of the total variation, with health problems minimized at zoos with warm, wet climates (Fig. 3-5c). Foot and skin problems were the two most common health problems for Indian rhinos. Climate Prin1, along with minimum indoor area, bore a relationship with foot health ($G^2 = 10.88$, 2 df, $P < 0.01$). The odds of foot problems increased in colder climates and as the minimum indoor area increased. Interestingly, foot problems were positively correlated with the complexity index, though the relationship was weak ($G^2 = 3.77$, 1 df, $P = 0.05$).

Several variables were correlated with skin health, but no single model was identified that best explained this health problem. Increases in complexity index ($G^2 = 4.51$, 1 df, $P = 0.03$), presence of grass substrate ($G^2 = 5.10$, 1 df, $P = 0.02$), area per individual ($G^2 = 5.67$, 1 df, $P = 0.02$), and minimum indoor enclosure area ($G^2 = 4.60$, 1 df, $P = 0.03$) reduced the frequency of skin problems. Combined models including these variables were significant ($P < 0.05$), but usually rendered one or both of the variables insignificant, indicating positive correlations among these factors (Spearman's Rho $P < 0.05$). A combined model of Climate Prin2 and mean exhibit area also explained skin health ($G^2 = 7.18$, 2 df, $P = 0.03$), though individually neither variable was significant. In general, zoos in warmer, wet climates with larger exhibit areas tended to experience fewer skin problems among their Indian rhinos.

DISCUSSION

Black, white, and Indian rhinos appear to respond differently to their captive environment. Demographic problems exist for both black and white rhinos, resulting in non-sustainable captive populations [AZA Rhino Advisory Group, 2002]. While reproduction tended to be high, black rhinos had the highest frequency of health problems and high mortality rates. White rhinos presented the reverse scenario, having low reproduction rates and a low frequency of health problems. Indeed, successful reproduction has occurred mainly among a small proportion of the founder population, with many individuals exhibiting reproductive abnormalities [Patton et al., 1999; Brown et al., 2001; AZA Rhino Advisory Group, 2002; Carlstead and Brown, 2005]. Conversely, the captive population of Indian rhinos appeared to be performing well demographically, which is supported by studbook analyses [AZA Rhino Advisory Group, 2002]. However, the international captive Indian rhino population has experienced high juvenile mortality rates and showed evidence of outbreeding depression, due to the low genetic diversity of captive Indian rhinos [Zschokke et al., 1998; Zschokke and Baur, 2002]. In this study, the frequency of health problems, particularly foot and skin problems, was relatively high.

Black Rhino

Climate, exhibit area, and number of individuals held at a zoo were identified as important explanatory variables for black rhino reproduction, mortality, and health. Given that black rhinos are a tropical/subtropical species, the fact that the North American temperate climate has an effect is not surprising. Higher birth rates were found in zoos located in warm, high precipitation regions with little seasonal variation. These regions more closely resemble the climate of their native range (Fig. 3-1). Hediger [1965] noted that temperature, day length, and humidity can greatly affect successful reproduction. While individuals are able to tolerate a wide range of climatic conditions, the range of optimal conditions for reproduction is typically much narrower [Begon et al., 1990]. Climate is also correlated with other enclosure and husbandry variables, such as the amount of time outdoors and exhibit area. Zoos in colder regions keep animals indoors during inclement weather [Fouraker and Wagener, 1996], which can extend for several months for some zoos. O'Connor [1986] suggested that this difference in husbandry practices possibly accounted for the longer mean birth intervals and fewer births at Whipsnade Park, Great Britain compared to San Diego Wild Animal Park, United States.

Zoos with a more "tropical" climate also tended to have a larger mean exhibit area (Climate Prin2; Spearman's Rho = 0.4476, P = 0.01). Carlstead et al. [1999a] found a positive relationship between the natural log of enclosure area and an institution's breeding success. In this study, exhibit area showed a nonlinear relationship with black rhino reproduction. A minimum outdoor enclosure space of 583 m^2 was associated with higher birth rates, but a threshold was reached at approximately 1048 m^2. Increasing mean exhibit area beyond this threshold did not confer any additional reproductive advantage.

Climate and exhibit area also were associated with mortality, but in an unexpected way. The conditions that lead to increased reproduction appear to be associated with higher mortality. A positive linear relationship between birth and mortality rates substantiates this finding. This could possibly be due to juvenile mortality rates; approximately 16% of the total mortality for black rhinos occurs within the first 30 days [Foose, 2005]. It should also be noted that higher mortality rates occurred in very large exhibit sizes ($\geq$ 1115 m^2), which exceed the threshold identified for birth rates.

For exhibit sizes less than 1115 m^2, complexity was a factor, with lower mortality rates in more complex exhibits, containing multiple structural components (i.e., pools, mud wallows, trees, shrubs, and shelters) and topographical variation. Studies on laboratory animals have shown that "enriched" environments, with larger cage sizes and greater spatial heterogeneity, can improve neurological functioning [Rosenzweig and Leiman, 1968; Rosenzweig et al., 1978; Kempermann et al., 1997; Brown et al., 2003], reduce stress and aberrant behaviors [Marashi et al., 2004], increase mating success [Dukas and Mooers, 2003] and promote general physical and psychological well-being [ILAR, 1998]. Conversely, captive animals are known to develop various negative physiological and behavioral responses to small, sterile enclosures [Carlstead, 1996]. This interaction between exhibit size and complexity suggests that complexity may mitigate the effects of confined space for captive black rhinos.

Nevertheless, zoos with exhibit sizes greater than 786 m^2 had fewer health problems. In addition to exhibit area, the social environment may play a significant role in black rhino health. The frequency of health problems was greater in zoos that housed multiple males. Black rhino males are typically solitary [Hillman-Smith and Groves, 1994], so the presence of another male may cause stress and increased aggression. Carlstead and Brown [2005] found that stress hormone variability, fighting behaviors, and mortality were higher for breeding pairs kept together daily. While adult males are housed separately, visual, auditory, and olfactory communication may still occur. Zoos that house multiple males also may be more likely to keep breeding pairs together, particularly since a breeding pair has been the recommended group size for the husbandry of captive black rhinos [Fouraker and Wagener, 1996].

Furthermore, disease transmission may be density dependent [Altizer et al., 2003]. Neiffer et al. [2001] documented leptospirosis in two black rhinos, speculating that the second rhino acquired the disease directly from the first infected rhino or indirectly from contaminated mud wallows. Minimizing contact between infected animals and vaccination against leptospira were recommended to prevent disease [Neiffer et al., 2001]. In this study, two or more vaccinations reduced the frequency of health problems for zoos that kept multiple males. However, this does not signify that the more vaccinations, the better. In a competing model, four or more vaccinations were found to be associated with higher mortality rates. Adverse reactions can occur [Fouraker and Wagener, 1996], so using caution when administering vaccinations may be prudent.

Similar to the health model, hemolytic anemia was associated with number of individual rhinos kept at an institution. As the number of individuals increased, the probability of hemolytic anemia increased. Interestingly, leptospirosis has been found in half of all cases [Fouraker and Wagener, 1996]. The percentage of alfalfa in the total diet also was linked with its incidence. Inadequacies in diet have been suspected as a cause of health problems [Miller et al., 1987; Fouraker and Wagener, 1996; Emslie and Brooks, 1999; AZA Rhino Advisory Group, 2002]. Black rhinos are browsers, but browse comprised a very small percentage of their diet (Table 3-5). The majority of their diet was composed of alfalfa, mixed grass hay, and commercial pellets. Grant et al. [2002] found similar results for the captive black rhino diet, with the following average percent composition: 61% hay, 28% pellet, 6% produce, and 5% browse. An exclusive alfalfa diet has been discouraged, but a mixture of legume and grass hays, supplemented with browse, has been the recommended diet [Fouraker and Wagener, 1996; Fouraker, 1997]. Alfalfa differs nutritionally from grass hay, by having higher lignin, crude protein, calcium, magnesium, and sulfur and lower neutral detergent fiber, manganese, and zinc [Oftedal et al., 1996; Van Soest, 1996]. High amounts of alfalfa in the diet are known to cause colic, diarrhea, and mineral imbalances [Fouraker and Wagener, 1996]. Differences in vitamin and mineral concentrations between wild rhinos, consuming a browse diet, and captive rhinos have been found, which may account for some of the diseases expressed in captivity [Clauss et al., 2002a; Dierenfeld et al., 2005].

While hemolytic anemia was one of the leading causes of death for captive black rhinos, particularly between 1976 and 1980, Dennis [2004] found that it is not currently a major health issue. Of the zoos surveyed, 67% reported no incidences of hemolytic anemia, with the remainder primarily reporting rare occurrences. Skin problems, however, are a significant health problem for black rhinos, but unfortunately no associations could be identified.

White Rhino

In contrast to their fellow African rhino species, social groupings, density, and diet appear to be important factors for white rhinos. White rhinos display the most social behavior of the rhino species. Females have overlapping home ranges and commonly aggregate in small groups ranging from a single female and her calf to multiple females and subadults [Groves, 1972; Owen-Smith, 1974; Fouraker and Wagener, 1996]. While most associations between subadults are temporary, the groupings may serve an important function by reducing aggressive attacks by territorial bulls and aiding in dispersal [Shrader and Owen-Smith, 2002]. Although mainly solitary, dominant territorial males will tolerate inferior or subadult bulls, which may coinhabit the territory [Owen-Smith, 1974; Fouraker and Wagener, 1996]. In captivity, the minimum recommended grouping for breeding is at least two females and one male, with a herd of four females, one male, and an extra male held separately, being preferred [Fouraker and Wagener, 1996].

I found that zoos holding more than two males had higher reproductive rates. Lindemann [1982 in Emslie and Brooks, 1999] found a similar result for white rhinos in captivity, with females having lower reproductive success if there was only a single male. Patton et al. [1999] speculated that mate choice was important for the reproductive behavior of females since their home ranges in the wild can include territories of several different males. Besides preferentially selecting territorial males, more females were found present in territories held by large bulls with large horns [Kretzschmar, 2002]. Furthermore, limited evidence shows that white rhino females rarely reproduce if kept as single male-female pairs, but may successfully reproduce with the introduction of a new male [Patton et al., 1999]. Castley and Hall-Martin [2003], however, found that white rhino reproduction on private land in South Africa did not greatly differ between populations with more than one bull (66%) and a single bull (70%). The total population size per property, though, may have influenced this result [Castley and Hall-Martin, 2003].

In fact, the entire social structure may be a critical factor in the successful reproduction of this species. Hediger [1965] recognized that reproduction was often dependent on group size. In an examination of the causes of reproductive failure among captive born females, Swaisgood et al. [In press] found that captive born females were more likely to reproduce if housed with other wild born females, including their mother. In this study, the number of males was positively correlated with the number of females housed at a zoo (Spearman's Rho = 0.5537, $P < 0.01$), which may have contributed to the higher reproduction.

Besides number of individuals, density was associated with white rhino reproduction and mortality. For zoos that had fewer males, densities greater than 0.0021 individuals/m^2 showed higher birth rates. This result is contrary to density-dependent reproduction, where fecundity has been shown to decrease with increasing density [Mduma et al., 1999; Coulson et al., 2000; Focardi et al., 2002; Rödel et al., 2004]. Negative density dependent effects in populations can be caused by competition for depleting resources at higher densities. In captive environments, competition is negligible, since food and other resources are supplied. The higher densities may in fact serve an important function for social species. Johnson et al. [2000] showed that social mustelids, with larger breeding group sizes, actually had smaller home range sizes than solitary populations. In addition, white rhino males that had a high frequency of females within their territory had greater mating success than males with territories where females spent less than 70% of their time [Kretzschmar, 2002].

This positive relationship between density and a component of fitness (i.e., reproduction) could represent an Allee effect, as defined by Stephens et al. [1999]. Allee effects typically emerge at low population sizes, when competition is minimal, as a result of demographic or genetic stochasticity, or facilitation among individuals [Courchamp et al., 1999]. Sociality and spatial distribution of a species may actually be a measure of Allee effects on individual fitness [Stephens and Sutherland, 1999]. Based on the relationship between Allee effects and mating systems, Stephens and Sutherland [2000] speculated that "if mate choice is restricted in small or low density populations, then low parental investment and low reproductive output may result. Such a phenomenon would certainly correlate with low reproductive rates and success in many species of zoo animals..."

The interaction between group size, enclosure area, and Allee effects may be an important determinant for white rhino social structure and spacing, and subsequently their breeding success and mortality. Both exhibit area and density were correlated with mortality. Zoos that had a mean exhibit area less than 1858 m^2, with greater than 376 m^2 per individual, had the lowest mortality rate. Reducing exhibit area would increase density, but mortality was higher in densities above 0.0027 individuals/m^2. This potentially indicates a non-linear relationship between mortality and density, with a threshold reached at approximately 376 m^2 per individual. Exceeding this threshold, negative density-dependent mechanisms may be operating, such as increased aggression between individuals [Poole and Morgan, 1973], increased stress [Arakawa, 2005; Carlstead, 1996], or increased disease transmission [Altizer et al., 2003]. Densities in captivity are on average several times higher than those in the wild, which can vary from 0.23 to 5.7 individuals/km^2 [Kretzschmar, 2002]. The optimal area per individual for reproduction and mortality may lie somewhere between 376 and 470 m^2 in the captive environment. This reflects a balance between Allee effects and negative density dependence, which can produce maximum population growth and ecological fitness at intermediate population densities [Courchamp et al., 1999; Stephens and Sutherland, 1999; Stephens et al., 1999].

The number of vaccinations also was important for reducing mortality in large exhibits. Several different reasons could explain this result. First, the number of individuals is positively correlated with exhibit size (Spearman's Rho = 0.4726, $P < 0.01$). Even though density is reduced in larger exhibits, the total number of individuals may be a more significant factor for disease transmission in zoos. Social structure and mating behavior can influence the opportunities for disease transmission, with larger group sizes and promiscuity increasing the risk of infection [Altizer et al., 2003]. Furthermore, individuals may be exposed to more pathogens in larger, naturalistic exhibits. For example, ticks, which are potential disease vectors, are known parasites of white rhinos [Groves, 1972]. Stoebel et al. [2003] detected Lyme disease, a tick-borne illness, in approximately 10% of the various captive ungulate and carnivore species tested, with differences in prevalence found between species and zoos. This difference was in part attributed to the degree of exposure, which is determined by its captive environment and its suitability for tick infestations.

The frequency of health problems, however, was mainly determined by diet. Diets composed of 40% or more pelleted feed were associated with increased health problems. White rhinos are grazers, selecting high quality grass species when foraging [Groves, 1972; Kretzschmar, 2002]. In zoos, the diet of white rhinos primarily consisted of mixed grass hay and pellets (Table 3-5). Pelleted feeds are recommended to provide nutritionally balanced diets, but only 25-40% of the total diet [Lintzenich and Ward, 1997] or less than one-third of the total calorie intake [Fouraker and Wagener, 1996] are advised. Gastrointestinal problems are known to result from excessive consumption of pellets, which lack the necessary fiber for digestion [Oftedal et al., 1996].

Furthermore, zoos that provided produce as a part of the diet reported more health problems. For instance, skin problems were found to be associated with percent produce and keeper time. As the percent of produce increased, the odds of skin problems greatly increased by several orders of magnitude. Fruits and vegetables are not a natural component of their diet, but have been suggested as beneficial [Fouraker, 1997]. Most commercial produce provided in captivity, however, is low in plant fiber and high in sugars, which can cause digestive problems [Oftedal et al., 1996]. Thus, Oftedal et al. [1996] cautioned against providing fruit and recommended that vegetables only be used moderately in herbivore diets. The recommendation to restrict the use of produce seems appropriate for white rhino diets, considering that even small amounts of produce were associated with increased frequency of health problems.

Keeper time was also a useful predictor of skin problems. As the amount of time that keepers spent per day increased, the probability of skin problems occurring increased. Thompson [1989] found that vigilance towards zookeepers was greater for larger sized ungulates, particularly females, and that the proportion of time spent foraging decreased when keepers were in the enclosure. Stress was suggested as a possible cause for this reduction in foraging behavior. The findings of Carlstead and Brown [2005] appear to support this assertion that keepers are a source of stress. White rhinos that showed fewer "friendly to keeper" behaviors, such as allowing touching, had higher mean corticoid levels [Carlstead and Brown, 2005]. As added evidence for stress, I found that stereotypic behavior was more likely as keeper time increased ($G^2 = 4.20$, 1 df, $P = 0.04$). Chronic stress is known to cause multiple adverse physiological effects, such as immune suppression and delayed wound healing [Carlstead, 1996; Dhabhar, 2000; French et al., 2006]. Given that increased chances of infection and slower rates of healing can both influence skin health, as well as the general health of the animal, the correlations between skin health, reactions to keepers, and stress should be further evaluated.

Finally, skin problems and the overall frequency of health problems were related to climate. In general, warm, wet climates appeared to be more conducive to white rhino skin health. Like black rhinos, this climate reflects the one in their native range (Fig. 3-1). The relationship between climate and frequency of health problems, however, was not as direct, with zoos in warm, dry climates experiencing more problems than zoos in cooler, wet climates. Climate Prin 2 was marginally correlated with the percent of pellets in the diet (Spearman's Rho = 0.2842, $P = 0.08$), indicating that zoos in warmer, wet climates tended to feed a greater proportion of pellets. Considering the effect of diet on health, this may explain the lower frequency of health problems in cooler climates. Moisture also might be the key factor, since Climate Prin 2 was associated with both skin and overall health. Examination of each of the individual climatic variables (i.e., temperature and precipitation), however, did not reveal any significant relationships with frequency of health problems. Thus, diet appears to be a better predictor for frequency of health problems in white rhinos.

Indian Rhino

Due to the smaller dataset for Indian rhinos, complex relationships among the explanatory variables and reproduction, mortality, and health could not be thoroughly examined. However, climate and husbandry variables, such as number of feedings and time spent by keepers, were identified as important factors in the response of Indian rhinos to their captive environment.

Reproduction was related to the number of feedings per day, with higher birth rates when food was provided continuously instead of separated into one or two feedings per day. Captive diets were mainly composed of mixed grass hay (Table 3-5) and composition did not significantly differ between the two feeding regimes (Kruskal-Wallis tests, $P > 0.05$). The digestive tract morphology, forage quantity and quality, and/or Indian rhino behavior, however, could potentially account for the observed relationship between birth rate and number of feedings. Like all rhinos, Indian rhinos are nonruminant, hindgut fermenters [Owen-Smith, 1988; Oftedal et al., 1996; Van Soest, 1996]. Food intake is restricted by longer retention times in their digestive tract, which allow greater fermentation and digestion of fiber [Owen-Smith, 1988]. Clauss et al. [2005a] recorded mean retention times of particles for Indian rhinos at 61 hours, the longest time recorded for hindgut fermenters. Given the slower food passage rates, the continuous feeding regime may facilitate efficient digestion. Lower digestive efficiency can affect nutrient absorption [Van Soest, 1996; Clauss et al., 2005b], leading to potential nutrient deficiencies, which are known to negatively affect reproduction [Asa, 1996; Hutchins et al., 1996; Wildt, 1996].

Alternatively, the increased availability of food may allow individuals to selectively consume a higher nutritive diet [Van Soest, 1996]. In other words, if the "salad bar" is always open, individuals have the opportunity to select higher quality, more palatable items among the food offered. Increases in food quantity and quality are known to increase reproduction [Asa, 1996; Hutchins et al., 1996; Geisser and Reyer, 2005]. However, Clauss et al. [2005b] estimated that digestible energy intake for captive Indian rhinos was well above required metabolic levels, even for some individuals on a roughage-only diet. Because unlimited food and increased weight gain can result in health and reproductive problems, Clauss et al. [2005b] cautioned against husbandry guidelines for the provision of *ad libitum* hay [Fouraker and Wagener, 1996; Fouraker, 1997], and recommended a restricted diet. Consequently, the relationships among feeding regime, food availability, diet selection opportunities, and reproduction are unclear.

Lastly, the behavioral response of Indian rhinos to a continuous feeding regime may have influenced the resulting pattern in birth rates. Concentrated feedings may reduce feeding times and create boredom, frustration, and/or stress, all of which can produce negative effects, such as stereotypic behavior [Carlstead, 1996; Swaisgood and Shepherdson, 2006]. For captive tapirs, the availability of food and natural vegetation tended to increase activity levels and reduce resting periods during the day [Seitz, 2001]. Oftedal et al. [1996] recommended using hay in herbivore diets since it prolongs foraging activity, which in turn may deter aberrant behaviors. Similarly, Carlstead [1996] recommended the use of feeding enrichment to improve captive animal welfare. Although in a meta-analysis, Swaisgood and Shepherdson [2006] did not find any significant differences in the efficacy of feeding versus non-feeding enrichment strategies. Whether the concentrated feeding regime is associated with stress is uncertain, but stress can reduce reproduction [Christian, 1956; Christian and Davis, 1964; Asa, 1996; Carlstead, 1996]. Unfortunately, I was unable to detect any relationship between presence of stereotypy at a zoo and number of feedings or feeding enrichments.

Nevertheless, stress may be a factor in Indian rhino mortality. Similar to the results found for white rhino skin problems, increased time spent by keepers was associated with higher mortality rates. As stated previously, humans may cause stress for captive individuals. In fact, Lott and McCoy [1995] found that wild Indian rhinos were disturbed from foraging and became more vigilant during tourist visits, particularly when proximity was less than 12 m. While captive rhinos may be more habituated to humans than their wild counterparts, human-rhino proximity is also much closer in captive settings. Furthermore, Indian rhinos tend to be more solitary than black or white rhinos [Fouraker and Wagener, 1996], which may make them more intolerant of intrusions into their space. Carlstead and Brown [2005] found correlations between stress, the percent of public access, and mortality for black rhinos and between stress and behavior towards keepers for white rhinos. However, whether keeper time directly relates to stress as a causal mechanism for mortality has yet to be determined.

Keeper time may simply be a correlate for climate, since the time spent by keepers was found to increase in zoos located in cold, dry climates. Along with higher mortality, the frequency of health problems also increased in colder, drier climates. Skin and foot problems, specifically, were both associated with climate. For example, the likelihood of skin problems significantly decreased with larger mean exhibit areas and warm, wet climates. Skin problems, however, may be multi-causal since exhibit area was correlated with several other variables, including density and complexity. While mud wallows and pools are known to help maintain skin health [Laurie et al., 1983; Fouraker and Wagener, 1996; Fouraker, 1997], significant relationships could not be identified. However, the general trend was a decrease in skin problems with an increase in mud wallows and pools. Furthermore, a significant relationship was found between the complexity index, which includes mud wallows and pools, and skin health, with the probability of skin problems reduced with increasing complexity.

Whereas skin problems were less frequent in large, more complex enclosures, foot problems actually were found to increase with increasing complexity. However, climate and indoor area showed a stronger relationship with foot health. In a comprehensive study examining Indian rhino foot problems, von Houwald [2001] provided several possible reasons for this pathology: hard, abrasive enclosure substrates, weight problems of animals, diet and nutrient deficiencies, aggressive behavior of males, access to water, foot morphology changes that lead to chronic trauma vulnerability, and genetic predisposition. The fact that I found colder climates to be associated with foot problems is not surprising, considering that the husbandry of rhinos in cold climates necessitates increased time indoors on hard, concrete surfaces. The relationship between complexity and foot problems, however, was surprising, yet may reflect increased opportunities for foot trauma, particularly if individuals have already become abnormal "pad-walkers" [von Houwald, 2001]. The use of softer substrates in enclosures, such as mulch, grass, or bedding, and the provision of pools and mud wallows have been recommended to reduce the development of foot problems [Fouraker and Wagener, 1996; von Houwald, 2001]. Unfortunately, no relationships between foot problems and mud wallows, pools, or grass substrates were found, possibly due to our small dataset. von Houwald [2001] also recommended that all indoor enclosures contain a pool, since Indian rhinos are known to spend considerable time in and around water. Only two zoos in our study provided indoor pools for Indian rhinos and both zoos reported foot problems. I also found that the incidence of foot problems was higher in zoos with larger indoor areas. Minimum indoor area was not correlated with either climate variable, but may indicate a degree of exposure to hard surfaces. The larger concrete areas may allow increased movement and subsequent abrasions on their feet. von Houwald [2001] suggested that activity level played a role in the development of foot problems, pointing to the fact that 100% of the males in the study were afflicted with foot problems compared to only 53% of the females, which are know to be less aggressive than males. Indoor activity level may account for our finding, although more research is needed. Lastly, I was not able to identify any correlation between diet or number of feedings and foot health, despite the possible connection.

Implications

The intent of this study was to identify key factors important for the management of captive rhinos. While each rhino species responded differently to their captive environment, several factors emerged as potentially important husbandry considerations. For instance, both the African and Indian rhinos appeared to be affected by the temperate North American climate. Zoological institutions are not capable of altering their climate, but can try to further mitigate the effects of cold, dry weather through the use of water pools, heaters, and humidity controls.

Diet, in terms of composition and feeding regime, also appeared to have a significant effect, particularly on rhino health. Diet varied among rhino species, though it generally consisted of mainly hay and commercial pellets. Black rhinos have been the focus of diet inadequacies due to the low level of browse in their diet [AZA Rhino Advisory Group, 2002; Grant et al., 2002] and the possible lack of tannins [Clauss et al., 2002b; Clauss, 2003]. I found that high levels of alfalfa also may be problematic for black rhinos. For white rhinos, the proportion of pellets and produce were important for health. In fact, the use of produce in white rhino diets should be reevaluated given the correlation with health problems. In addition to diet composition, the feeding regime may be important for rhinos, specifically Indian rhinos. Considering its possible effect on reproduction and health, diet should be further examined for all rhino species.

While not all institutions have sufficient enclosure sizes recommended for breeding, the mean area per individual exceeded the minimum 139 m^2 required [Fouraker, 1997]. Rhinos may require large areas, but thresholds in enclosure size may exist. Exhibit sizes ranging between approximately 600 and 1100 m^2 may be important for the successful management of black rhinos, in terms of their reproduction, mortality, and health. Similarly, a range of densities, between 376 and 470 m^2 per individual, may be significant for white rhinos. Larger social groupings, however, appeared to be a greater influence on white rhinos, whereas black rhinos may respond better if kept more solitary. Indian rhinos are typically kept solitary except for breeding [Fouraker and Wagener, 1996] and I did not find any evidence that suggested this is inappropriate.

Finally, the relationship between husbandry variables and stress may be consequential for successful rhino husbandry. Density and human presence may be sources of stress, which could potentially account for the relationships observed in this study. For instance, zoos that kept two or more black rhino males reported a greater frequency of health problems. Moreover, a positive relationship between keeper time and health problems and mortality rates were found for white and Indian rhinos, respectively. Minimizing the time spent by keepers, or degree of human disturbance, may in fact be beneficial. However, the linkage between these variables, stress, and animal welfare still needs to be established. Indeed, further research is needed to determine the exact mechanisms that have created all of the patterns described in this study.

Other factors, such as vaccinations, complexity, and indoor area, were found to be related to rhino health, though to a lesser degree. Nevertheless, consideration should be given to their potential effect on captive rhinos for optimal captive management. Tradeoffs, however, may exist when attempting to optimize multiple response variables. For example, continuous feeding was associated with Indian rhino reproduction, but overweight individuals may experience more foot problems. Similarly, increases in complexity may reduce Indian rhino skin problems, but may increase foot problems. Reproduction was also positively correlated with mortality, so that improvements in the conditions for reproduction may increase mortality rate. In this case, efforts directed at reducing juvenile mortality may resolve this paradox. Unfortunately, higher infant mortality rates tend to be associated with larger, wide-ranging species [Clubb and Mason, 2003]. Considering the popularity of large animals, such as rhinos, in zoos [Ward et al., 1998] and the conservation role that zoos serve for these endangered species [Emslie and Brooks, 1999; AZA Rhino Advisory Group, 2002] continued effort should be invested in the improvement of captive breeding and management to attain sustainable populations.

CONCLUSIONS

1. Black, white, and Indian rhinos respond differently to their captive environment.

2. Climate appears to be an important factor for all three rhino species.

3. Nonlinear relationships were identified for exhibit area.

4. Socioenvironmental factors, such as the number of individuals and density, may be critical for the husbandry of white rhinos.

5. Diet composition was associated with health problems for black and white rhinos, while feeding regime was associated with Indian rhino reproduction.

6. Human presence may be a significant factor, given the relationships between time spent by keepers and rhino mortality and health.

7. Various other husbandry and environmental factors may be important for the successful management of rhinos. Table 3-6 summarizes the responses found for each of the rhino species.

8. The descriptive models for each of the rhino species can be used to better understand the patterns between the captive environment and rhino reproduction, mortality, and health and help guide captive management decisions.

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Table 3-1. Eigenvectors for the first two principal components of the climate principal components analysis.

Climate Variables	Principal Component 1	Principal Component 2
Days ≤ 32 F	0.56626	0.09526
Days ≥ 90 F	- 0.37340	0.46568
Mean annual temperature	- 0.56606	0.09608
SD temperature	0.46762	0.42004
Precipitation	- 0.02880	0.76708
Percent Variance Explained	58.68%	22.27%

Table 3-2. Summary of mean rhino reproductive rate, mortality rate, and weighted frequency of health problems for zoological institutions in North America.

	Black	White	Indian
N (zoos)	33	40	19
Reproductive Rate	0.0263 (σ = 0.0263)	0.0122 (σ = 0.0197)	0.0154 (σ = 0.0182)
Mortality Rate	0.0113 (σ = 0.0099)	0.0342* (σ = 0.1588)	0.0045 (σ = 0.0064)
Health Problems	5.7 (σ = 4.1)	2.6 (σ = 2.9)	4.6 (σ = 2.5)

* Two outliers identified; mean mortality rate excluding outliers equals 0.0053 (σ = 0.0068).

Table 3-3. Health problems by category for each rhino species, ranked by occurrence at zoological institutions in North America. Rare is defined as occurring infrequently in any individual; common is occurring multiple times for one individual or occurring in several individuals. The remaining percentages for each health problem reflect no occurrences.

Health Problems	Black	White	Indian	All
	% (n = 32)	% (n = 38)	% (n = 18)	% (n = 88)
Skin				
Rare	47	53	35	47
Common	38	3	35	22
Foot				
Rare	34	26	44	33
Common	9	5	39	14
Stereotypic Behavior				
Rare	41	26	47	36
Common	28	0	12	13
Eye				
Rare	22	37	18	28
Common	13	3	6	7
Diarrhea/Vomiting				
Rare	28	16	12	20
Common	9	3	0	5
Parasitic Infections				
Rare	9	18	24	16
Common	6	5	12	7
Oral				
Rare	31	8	12	17
Common	9	0	0	3
Hemolytic Anemia				
Rare	31	5	6	15
Common	6	0	0	2
Respiratory				
Rare	16	11	6	11
Common	6	0	0	2
Vasculopathies				
Rare	19	5	6	10
Common	6	0	0	2
Colic				
Rare	9	13	17	13
Common	0	0	0	0
Rectal Prolapse				
Rare	0	5	17	6
Common	0	0	6	1

Table 3-4. Summary statistics for enclosure and husbandry variables for each of the rhino species.

	Black (n = 33 zoos)		White (n = 40 zoos)		Indian (n = 19 zoos)	
Continuous Variables	Mean	SD	Mean	SD	Mean	SD
# Males / zoo	1.7	1.0	1.9	1.7	1.2	1.0
# Females / zoo	1.2	0.8	2.2	2.6	1.6	2.9
Exhibit Area (m^2)	1309.5	1739.0	85155.5	326802.3	24060.8	64757.0
Minimum Indoor Area (m^2)	33.1	18.3	72.3	146.9	35.2	13.7
Area (m^2) / individual	865.0	830.3	14480.1	50363.1	20563.2	71186.5
Complexity Index	4.4	1.4	5.1	1.6	4.9	1.5
Outdoor Pools	0.5	0.5	0.7	0.9	1.0	0.7
Mud Wallows	1.2	0.8	2.6	4.1	1.7	2.2
Public Perimeter (%)	31.5	18.0	35.9	26.3	26.7	14.5
Keeper Time (hrs.)	4.1	2.5	3.5	2.9	4.1	3.1
Vaccinations	1.8	1.6	1.2	1.5	1.3	1.5
Categorical Variables	Probability		Probability		Probability	
# Feedings / day (continuous vs. 1-3x)	0.34		0.29		0.56	
% Walls (>50% vs. ≤50%)	0.19		0.23		0.11	
Grass substrate (presence vs. absence)	0.52		0.63		0.58	

Table 3-5. Summary of the diets for each of the rhino species at the North American zoos included in this study. Mean percentage and standard deviation of each diet category are provided; total diet percentage may not equal 100% due to rounding errors.

Diet Composition	Black (n = 32)		White (n = 39)		Indian (n = 18)	
	%	SD	%	SD	%	SD
Alfalfa	34	25.8	15	21.1	3	8.4
Mixed Grass	28	25.5	58	26.4	67	18.3
Commercial Pellets	26	19.5	24	15.6	19	17.7
Browse	7	9.6	1	3.7	4	4.8
Produce	5	4.9	2	3.4	6	3.6

Table 3-6. Responses of each of the rhino species to the husbandry and environmental factors in North American zoos. Direction of the response is indicated by a "+" for a positive relationship or "–" for a negative relationship for reproduction (R), mortality (M), and health problems (H).

	Black			White			Indian		
Zoo Variables	R	M	H	R	M	H	R	M	H
Climate (Prin 1 or 2)	+	+				-§			-§‡
# Males / zoo			+	+					
Total number of individuals / zoo			+*						
Exhibit Area (m^2)	+/-	+	-		+				-§
Minimum Indoor Area (m^2)									-§ +‡
Area (m^2) / individual				-	-				-§
Complexity Index		-							-§
Keeper Time (hrs.)						+§		+	
Vaccinations			-		-				
# Feedings / day (continuous vs. 1-3x)							+		
Diet									
% Pellets						+			
% Alfalfa			+*						
% Produce						+§			
Grass substrate (presence vs. absence)									-§

* hemolytic anemia; § skin problems; ‡ foot problems

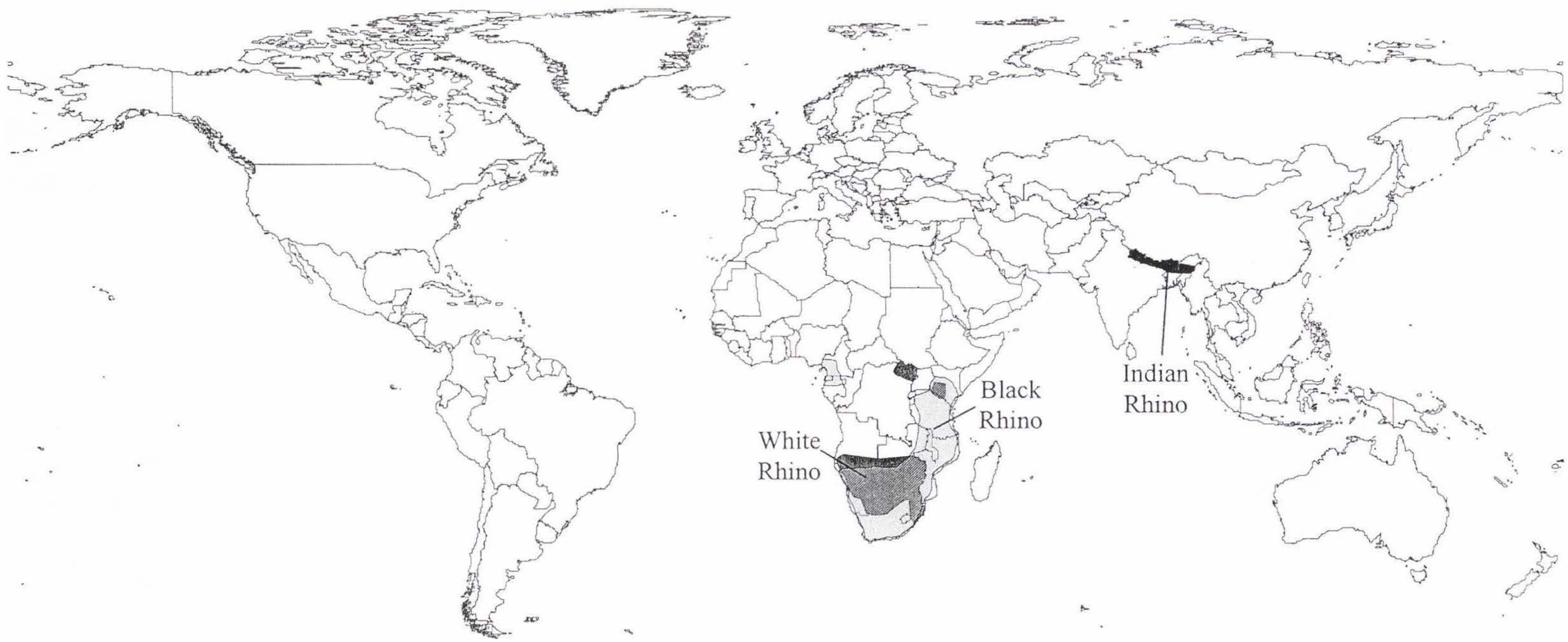

Fig. 3-1. Distribution map of black, white, and Indian rhinos [Fouraker and Wagener, 1996; Foose and van Strien, 1997; Emslie and Brooks, 1999]. Shaded regions represent extent of distribution; actual distribution is highly fragmented within these regions.

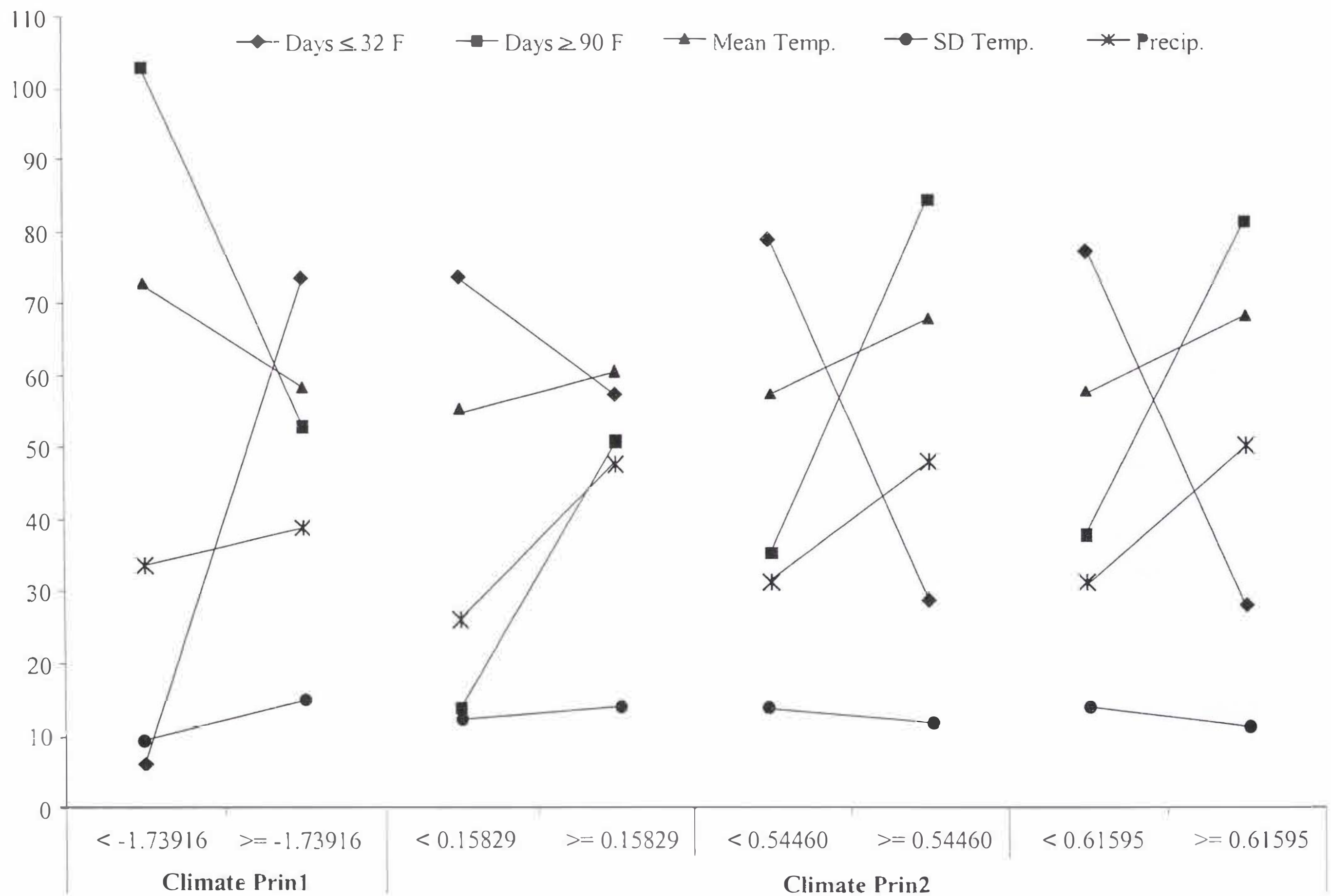

Fig. 3-2. Summary of climatic data for CART node values of Climate Prin1 and Climate Prin2. Average values are given for each of the climatic variables: mean number of days with a minimum temperature of 32° F or lower, mean number of days with a maximum temperature of 90° F or higher, mean annual temperature (°F), standard deviation of normal daily mean temperature, and mean normal precipitation (in.).

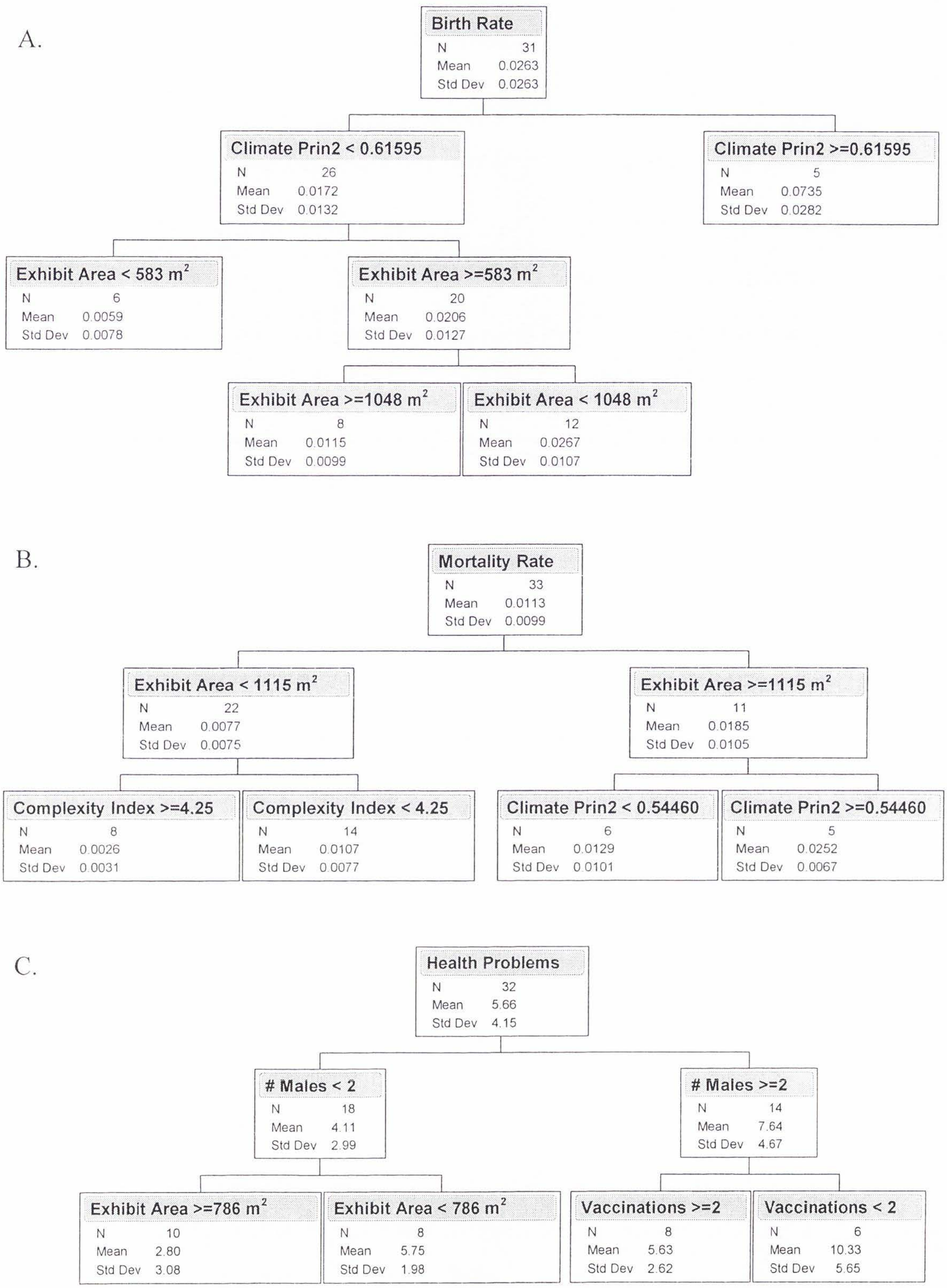

Fig. 3-3. CART diagrams for black rhino reproduction (A), mortality (B), and health (C).

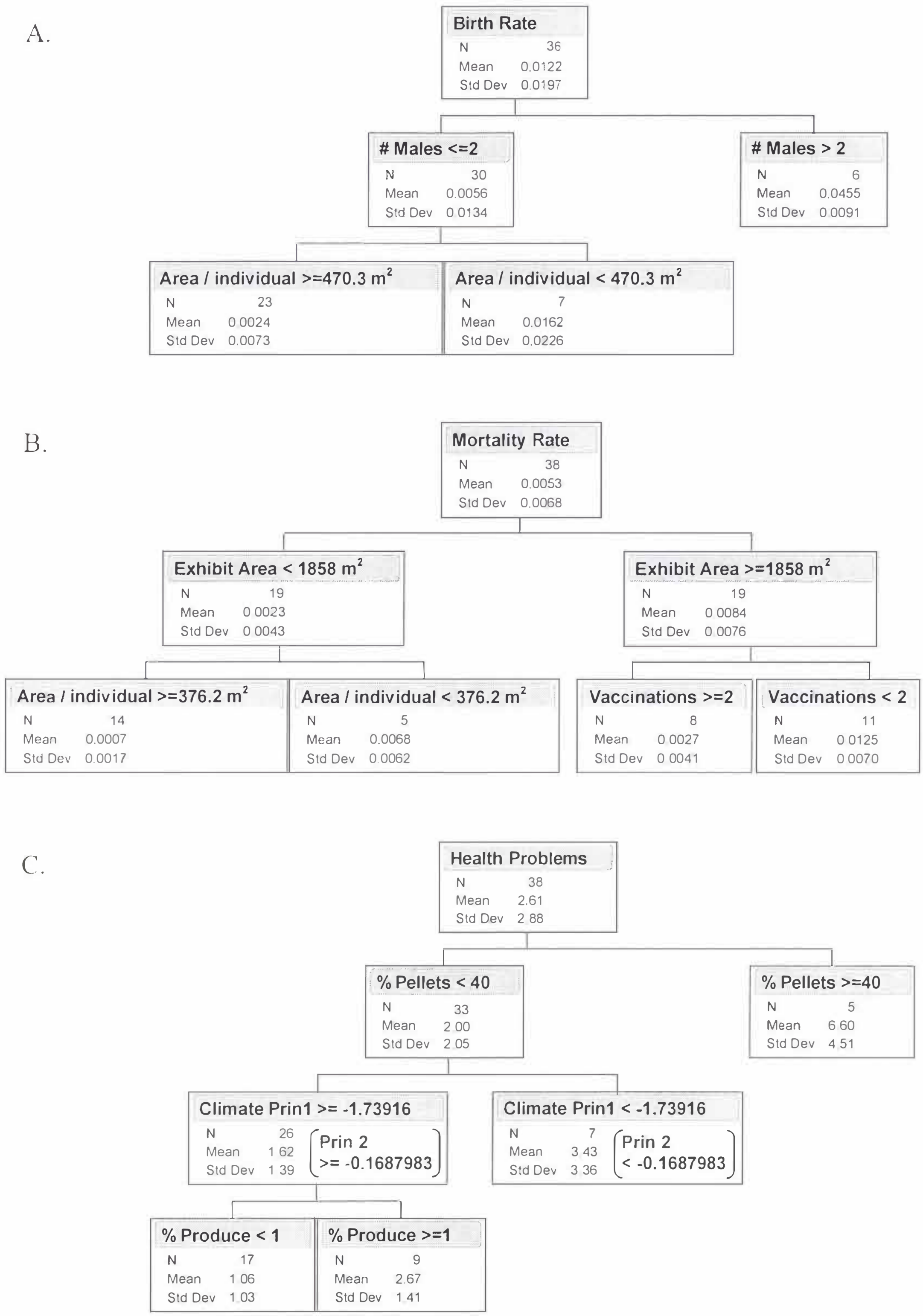

Fig. 3-4. CART diagrams for white rhino reproduction (A), mortality (B), and health (C).

A.

B.

C.

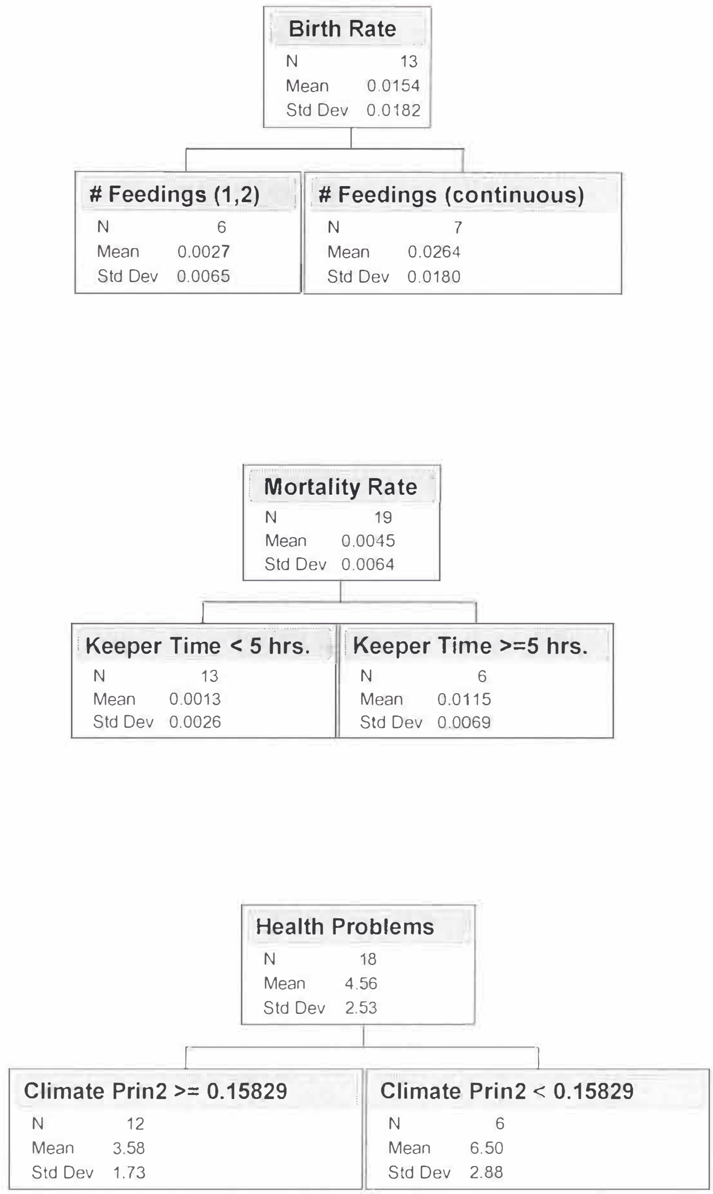

Fig. 3-5. CART diagrams for Indian rhino reproduction (A), mortality (B), and health (C).

CHAPTER 4

CONCLUSION

The objective of this study was to identify key elements in the captive environment that were associated with reproduction, mortality, and health of tapirs and rhinos in North American zoological institutions. Relationships between various husbandry factors and species response were found, that could help guide captive management decisions. The importance of each of the explanatory factors, such as density, exhibit size, structural complexity, diet, and climate, depended on both the species, or family group, and specific response (i.e., reproduction, mortality, and health). The observed correlations, however, do not necessarily indicate a causal relationship, but rather indicate aspects that need further examination.

Different analysis techniques were used for tapirs and rhinos because of differences in the datasets. Multiple linear regression was used for the larger tapir dataset, whereas nonparametric modeling was used for the individual rhino species datasets, which did not satisfy the assumptions of parametric statistics. Each statistical tool had its own advantages and disadvantages. By using Akaike's information criterion for model selection among the set of tapir regression models, I was able to evaluate the weight of evidence for each model, more reliably identify the best model(s) in the set, and rank the importance of each variable [Burnham and Anderson, 2002]. This technique, however, was somewhat limited for exploratory data analysis. Selecting the set of candidate models can be challenging if little is known about the system. Furthermore, the number of a priori models that can be appropriately evaluated is restricted by the size of the dataset. Even exceeding this limit, valuable models may have been left out of the model set. Classification and regression trees allowed for greater flexibility. However, choosing the appropriate model, or tree size, was more complicated due to problems with model stability and over-fitting the data. For this reason, cross validation techniques were used to help determine the most parsimonious model that best fit the data. Despite their differences, both statistical analyses for tapirs and rhinos yielded informative and useful results.

The three tapir species [i.e., Baird's (*Tapirus bairdii*), South American (*T. terrestris*), and Malay (*T. indicus*)] were found to respond similarly to their captive environment. On average, tapirs have been successfully managed, with stable or increasing captive populations. Zoological institutions with more enclosures, greater overall exhibit complexity, and more individuals housed and transferred, tended to have higher reproductive rates. No significant correlations were found between tapir mortality and their captive environment, though mortality did appear to be related to their health. Health problems tended to decrease with decreasing density, increasing variation between outdoor and indoor enclosure sizes, and increasing public perimeter. Mud wallows were associated with fewer skin problems, while climate was related to both eye and foot problems. Significantly correlated, exhibit size and complexity also were factors in tapir health and together may be important for tapir management.

Each rhino species, on the other hand, responded differently to their captive environment. Moreover, the captive populations of black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinos have been demographically unstable. The need for new individuals from the wild to supplement declining captive populations undermines the conservation goals of zoos and further exacerbates the endangered status of these species. While the captive population of Indian rhinos (*Rhinoceros unicornis*) is self-sustaining, Indian rhinos have experienced numerous foot and other health problems. Factors potentially important for captive rhino management included climate, exhibit area, social groupings, enclosure complexity, diet, human presence, and vaccinations. Climate was correlated with reproduction, mortality, or health for all three rhino species, with warmer, wet climates seemingly better suited for rhino husbandry. In addition to climate, black rhinos appeared to be responding to exhibit size and number of individuals, particularly males. This is likely due to the primarily solitary behavior of males in the wild. White rhinos, however, showed evidence of social grouping requirements for successful reproduction. Although Indian rhinos are more successfully managed, possible improvements could be made by altering feeding regime, reducing time spent by keepers, increasing exhibit size, and minimizing area and time on hard indoor surfaces. Special considerations for each rhino species are needed to help improve reproduction, lower mortality rates, and prevent health problems.

The following question then remains: why do captive rhinos experience reproductive failure, high mortality, and numerous health problems whereas tapirs are, in general, successfully managed in captivity? Multiple reasons may explain this phenomenon. First, there is obviously a size difference between these two groups. Rhinos are approximately five to six times the size of tapirs in terms of body mass. Indian and white rhinos, the largest rhino species, range in size from 1,800 to 2,200 kg

[Fouraker and Wagener, 1996], whereas the largest tapir species, the Malay tapir, can weigh 450 kg [Barongi, 1993]. Clubb and Mason [2003] found that carnivores with larger home range sizes experienced higher infant mortality and stereotypic behavior in captivity. Similar to their findings, rhinos in this study had a higher incidence of stereotypic behavior than tapirs (Tables 2-7, 3-3).

Home range sizes can vary considerably depending on resource availability, resource distribution, organism traits, species interactions, and other factors. However, as initially demostrated by McNab [1963], home range size tends to scale allometrically with body size in the following form:

$$H = Y_0 M^b \qquad \text{(Eq. 1)}$$

where H is home range size, M is body mass, Y_0 is a constant, and b is the scaling exponent or slope. Home range sizes for tapir and rhinos have been reported between 1 to 12.75 km^2 and 2 to 133 km^2, respectively [Groves, 1972; William and Petrides, 1980; Laurie et al., 1983; Hillman-Smith and Groves, 1994; Brooks et al., 1997; Foerster and Vaughan, 2002; Kretzschmar, 2002; Medici et al., 2003]. McNab [1963] originally proposed that home range size would scale to the ¾ power in relation to metabolic rate and body mass. This allometric scaling law has been repeatedly examined and adjusted to try to account for deviations [e.g., Swihart et al., 1988; Holling, 1992; Haskell et al., 2002]. Constructing a model that incorporated the resource distribution and structure of the environment, Haskell et al. [2002] concluded that the scaling exponent should vary over a range of 3/4 to 11/12 for herbivores in a two-dimensional environment. Applying this theory in the captive environment to assess how closely enclosure sizes scale to body mass and home range size may prove informative.

Mean body size and median exhibit sizes were used to calculate the scaling exponent observed in captive environments (Fig. 4-1). Not surprisingly, the scaling exponent ($b = 0.52$) was much lower than the range predicted by Haskell et al. [2002]; if enclosure sizes scaled similarly to home range sizes, the scaling exponent should be between 0.75 and 0.92. The lower scaling exponent for tapir and rhino enclosures indicates that the proportional increase in enclosure sizes is approximately 30% or more below the allometric scaling pattern observed in nature. Thus, the larger rhino species appear to have less space available in captivity as a function of their body size compared to tapirs. Exhibit size as a proportion of home range size, however, did not significantly decrease with body size ($F_{1,4} = 0.62$, $P = 0.47$; Fig. 4-2). Consequently, differences between the captive populations of tapirs and rhinos cannot be solely explained by differences in space allocation in relationship to their body mass and home range size, although it may contribute to some of the problems experienced by captive rhinos. As noted in the previous chapters, enclosure size was found to be a key factor for both tapirs and rhinos in captivity.

Another possible reason why captive management of tapirs has been more successful than rhinos is the species level differences among rhinos. A cookie cutter approach to captive rhino management would not work for all rhino species since each has their own requirements. For example, black rhinos are browsers and have specific dietary needs. Being fed a standard grazing diet used for the other rhino species has created problems [Fouraker and Wagener, 1996]. In this study, I found that higher levels of alfalfa were associated with the incidence of hemolytic anemia. Furthermore, social behavior differs between rhino species. Unlike the pattern shown for black or Indian rhinos, reproductive rate for white rhinos was higher with more males and higher densities. Conversely, tapirs have very similar life history traits and ecological requirements. This coupled with their smaller size may contribute to their relative ease of management in captivity.

Interestingly, the main health problems experienced by rhinos were the same as for tapirs; skin and foot problems were prevalent for both families. Climate appeared to play a major role, particularly for skin problems. Eye problems of Malay tapirs also were associated with climate. Both tapirs and rhinos are tropical/subtropical species, so the North American temperate climate may present suboptimal environmental conditions for these species. Special considerations to moderate the effects of climate, such as the provision of shade and adequate water sources, are needed to offset potential health problems.

As shown in this study, the environment provided within the zoo can be critical for the maintenance of self-sustaining captive populations and the conservation of wildlife species that are threatened with extinction in their native habitat. The relationships among the various factors that define the captive environment and species responses, however, are highly complex. Multiple interactions and correlations among variables make unraveling husbandry problems a challenge. Tradeoffs between factors, logistical constraints, and individual behavioral differences further confound the problem.

The patterns identified across the multiple zoological institutions in this study are intended to help elucidate key factors important for the successful management of captive tapirs and rhinos. An adaptive management approach should be employed to test the effects of these factors on reproduction, mortality, and health. While studbook data provide valuable life history information, similar databases should be kept regarding the specific husbandry procedures and enclosure design. Assessing the changes and effects over time may be critical, particularly for long-lived species such as tapirs and rhinos. Ultimately, this information can be used to improve husbandry guidelines and to bring us one step closer to reaching captive management and conservation goals.

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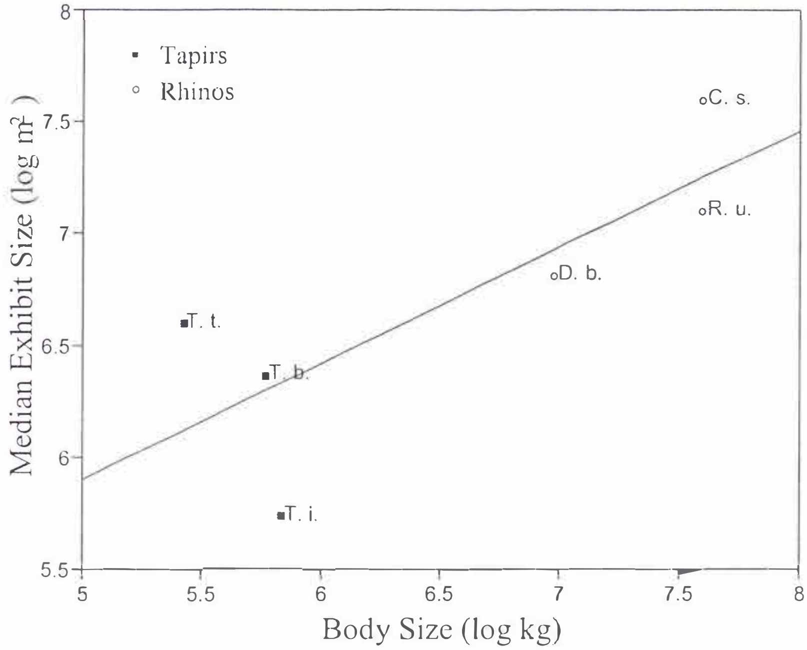

Fig. 4-1. Median exhibit size in relation to body size for rhino and tapir species. (Log Median Exhibit Size = 3.3122 + 0.5184 Log Body Size; R^2 = 0.64)

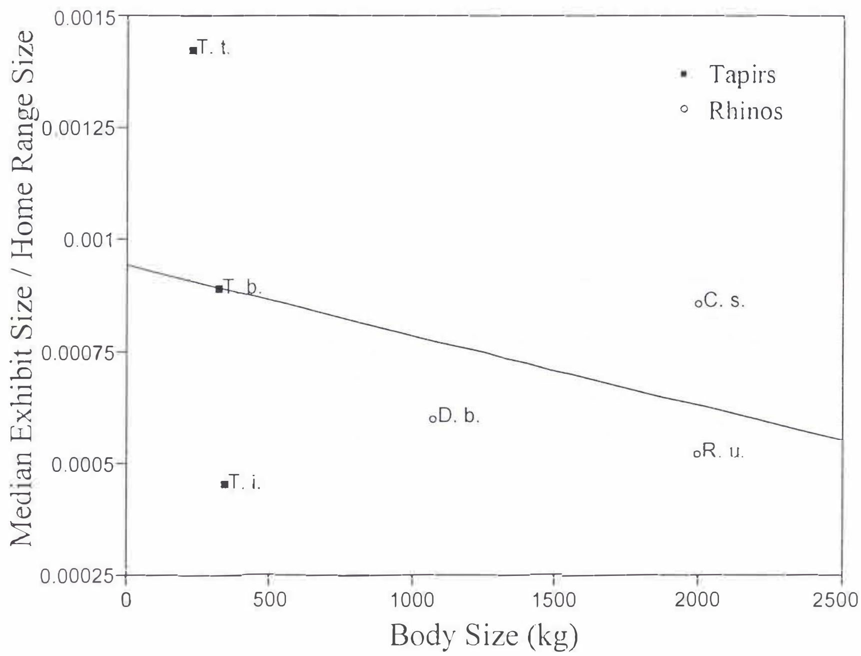

Fig. 4-2. Relationship between median exhibit size as a proportion of average home range size and body size. ($Y = 0.0009 - 1.555*10^{-7}$ Body Size; $R^2 = 0.13$)

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