Issues of captivity and conservation surrounding pantherine cats with a focus on the lion (*Panthera leo*) and the tiger (*Panthera tigris*)

A SENIOR THESIS PRESENTED TO

The Department of Organismic and Evolutionary Biology, Harvard University,
Cambridge, MA 02138

By: Karen R. Lovely

Thesis Advisor: Professor David Haig

March 2009

Acknowledgements

I would like to thank all of the organizations and individuals who supported my research and thesis.

For funding, I would like to thank the Harvard College Research Program.

For inspiration, brainstorming, feedback, and a shared enthusiasm for lions and tigers, I would like to thank Professor David Haig.

For his wonderful friendship and the generous advice he provided during the past four years, I would like to thank Professor Farish Jenkins.

For sharing their time and opinions, I would like to thank everyone who allowed me to interview them, especially Joan Galvin, Bhagavan Antle, Mindy Stinner, Zuzana Kukol, Timothy Santel, Pete Thomson, John Goldberg, and all of the affiliates of the Association of Zoos and Aquariums.

For their constant support and editing help, I would like to thank Mom, Dad, Ann, Pete, Dunbar, Rikka, April, Roxanne, and all my friends who have listened to me endlessly discuss lions and tigers.

Table of Contents

ABSTRACT

Thousands of lions and tigers live in captivity in the United States, residing in zoos, private exhibits, sanctuaries, research facilities, and family homes. As a result of limited federal and state management of the captive exotic cats, the total combined population of lions and tigers in the United States is unknown but estimated to be in the tens of thousands. Lions and tigers reside in captivity in staggering numbers, but the wild populations are in decline due to habitat loss and fragmented home ranges. Through population management, public education, and biological research, caretakers and conservationists hope that the captive population can assist in future wildlife conservation.

This thesis investigates the practices of the zoological facilities affiliated with the Association of Zoos and Aquariums, The Institute for Greatly Endangered and Rare Species, four large cat rescue sanctuaries, and multiple private owners. I sought to understand how the captive felines in each facility benefit public education, behavioral and physiological research, and in building a self-sustaining captive gene pool to serve as a backup population for the threatened wild species.

The results of my research display that lion and tiger caretakers are dedicated to conservation, but that there is a lack of collaboration between captive feline handlers. Keepers disagree on the importance of maintaining subspecies distinctions, the methods to pair mating partners, the techniques to prevent inbreeding, and on the priorities of captive populations to best aid conservation. Few captive facilities will publicly share medical records, data on reproductive success, or information indicating captive lion and tiger population dynamics. Without these records, it is difficult to assess which practices build stable populations. Furthermore, there are no records indicating the number of exotic felines in captivity in the United States, where they are housed, and in what conditions they live. Before further legislation is passed regulating captive exotic feline ownership, research investigating successful caretaking methods must be pursued, and collaboration between all captive *Panthera* owners must ensue, enabling the captive population to aid the preservation of the wild populations in the greatest possible way.

INTRODUCTION

A three-month-old tiger cub peered at me through an eight-foot high chain link fence. He wedged his black nose, moist and shiny, through a gap between the wires of the barricade. With a sudden twitch, his golden head turned, the eyespots on the rears of his ears wiggled, and he charged at a second cub, rolling in the dirt on the other side of the pen. Moments later, I sat in an audience of over 150 people at the King Richard's Faire in Carver, MA; the two cubs, along with several older tigers that were heavier by hundreds of pounds, walked onto a stage less than 40 feet away from me. Only a chain leash stood between the tigers and me.

Every October, over 100,000 Boston area residents have a similar experience watching the tigers at King Richard's Faire. Through a presentation on the "Tiger Stage" the audience learns about the natural habitat and wild habits of this endangered cat. Lions and tigers, because of their beauty and majesty, are considered a calling card of conservation, easily capturing the attention of a broad public audience. In captivity, these rare, endangered cats are accessible to groups ranging from elementary school students in Detroit and biology students in San Francisco to inner city residents in Houston. In circuses, zoos, sanctuaries, research facilities, and private homes throughout the United States, the African lion (*Panthera leo)* and the tiger (*Panthera tigris*) reside in great numbers. There are an estimated 5,000 to 20,000 tigers in captivity in the United States (57, 62, 89) compared to fewer than 7,000 tigers remaining in the wild (7, 56, 64). Lions also live in captivity in the United States, albeit in smaller numbers than tigers. No estimates predict how many lions reside in zoos and private facilities, but I suspect that there are at least 1,000 lions in captivity. Although it has a small captive population, the lion population in the wild is more stable than the tiger population; estimates indicate the wild population to be in the tens of thousands. The effective population size, however, may be drastically lower and in rapid decline (10, 12, 64). *Panthera* species have long been revered wild cats desired for their fur and bones, and powerful rulers have taken these wild cats as symbols of strength. Thus, it is with fear that we watch their populations rapidly decline in the wild.

Phylogeny

Panthera is monophyletic genus within the Felidae (order: Carnivora) and includes the tiger (*Panthera tigris*), lion (*P. leo*), leopard (*P. pardus*), jaguar (*P. onca*), and snow leopard (*P. uncia*) (68, 96). The pantherine cats include *Panthera* in addition to 16 other species. *Panthera* underwent a rapid evolutionary radiation during the Pleistocene, between one and eight million years ago, and has since radiated to the species that we now know as *Panthera* (65, 88, 96). Defining the phylogenetic relationships within the cat family has historically proven difficult due to their recent radiation. Recent molecular analyses have, however, helped uncover the phylogeny of the Felidae (65, 95, 96).

Scientists introduced molecular analysis in the mid-1990s as a method to determine the phylogenetic relationships within *Panthera*, but it has yet to present a clear and definitive phylogeny. The most recent analysis, using combined mitochondrial DNA and nuclear data, presents a well-resolved, strongly supported tree with the tiger placed as the sister species to other members of the genus and with the snow leopard embedded within *Panthera* (Appendix A, Image 3) (96). An earlier, less resolved tree sorted by partial 12S rRNA and cyt*b* genes also places the snow leopard within *Panthera*, but disagrees with Yu and Zhang on the position of the clouded leopard (*Neofelis nebulosa*), believing it to also lie within *Panthera* (Appendix A, Image 2)(48, 49). These more recent phylogenies challenge traditional phylogenies that place the snow leopard as a monotypic genus (Appendix A, Image 1) (64, 92). Molecular analysis has cleared up many questions about the relationships within *Panthera*, but further research is necessary to truly understand its phylogeny – a step necessary for conservation (17).

In this thesis, I focus on the lion and the tiger, two pantherine cats frequently found in captivity. The lion and the tiger are both divided into geographically, morphologically, and genetically defined subspecies. Researchers, however, debate the existence of these subspecies. Those supporting subspecies distinctions believe the genetic and morphological differences between tigers (and lions) from different geographic regions result from local adaptation and genetic drift. According to this thought, these

differences evolved during the Holocene when natural barriers isolated subpopulations of a single species (10, 23, 51, 55, 56). However, other scientists believe that subspecies distinctions are illusionary and result only from human interference. Tigers may have once lived in a habitat that was continuous over the entire tiger home range throughout Asia and southeast Russia. Natural selection acted on this population causing a cline, a morphological and genetic gradient over the entire range. A cline would not result in subspecies; rather, slow and continuous changes created the genetic and morphological variation. According to this idea, the current differences between tiger populations result from human activity that divided the continuous habitat, causing a loss of the intermediate populations that previously enabled a clinal gradient (51, 56).

Assuming the accuracy of the subspecies hypothesis, researchers have delineated eight subspecies of tiger originally distinguished by morphological variation and now recognized by molecular markers in mitochondrial and nuclear DNA (46, 51, 56, 64). These eight subspecies share a most recent common ancestor that lived between 72,000 and 108,000 years ago (56). Three subspecies, *P.t. balica* (Bali), *P.t. virgata* (Caspian), and *P.t. sondaica* (Javan) are recently extinct (51, 56, 64), and a fourth subspecies, *P.t. amoyensis* (South China tiger) exists only in captivity (93). Populations of the four other subspecies, *P.t. altaica* (Amur tiger), *P.t. corbetti* (Indochinese tiger), *P.t. sumatrae* (Sumatran tiger), and *P.t. tigris* (Bengal tiger) still live in the wild in areas of Asia and southeast Russia. Potential exists for a sixth extant subspecies within the Northern Indochinese tiger. The Isthmus of Kra divides the population of Indochinese tigers; recent genetic analysis shows the population has potentially split into two different subspecies: *P. t. corbetti* (Northern Indochinese tiger) and *P.t. jacksoni* (Malayan tiger) (56).

Researchers have classically split the lion into eight different subspecies based on geography and morphology: *Panthera leo persica* (Asiatic lion), *P.l. leo* (Barbary lion), *P.l. senegalensis* (West African lion), *P.l. azandica* (North East Congo lion), *P.l. nubica* (East African lion), *P.l. bleyenberghi* (Southwest African lion), *P.l. krugeri* (Southeast African lion), and *P.l. melanchaita* (Cape lion) (10). These subspecies share a most

recent common ancestor between 70,000 and 200,000 years ago (11). Both *P.l. leo* and *P.l. melanochaita* are extinct although some hybrid captive animals may carry their genes (11). Recent analysis of mitochondrial DNA, however, divides the lion into five subspecies rather than the classical eight. These subspecies are also geographically defined as subspecies unique to North Africa-Asia (Asiatic Lion), West Africa, Eastern Sahel, eastern-southern Africa, and South-western Africa (10, 23). The four subspecies in Sub-Saharan Africa are frequently referred to as the African lion rather than distinguished as subspecies.

Demographics

The tiger historically inhabited the Indian subcontinent throughout Asia from the Caspian Sea to the Aral Sea through Southeast Russia and the Sunda Islands (50, 56, 64). The tiger lives in a wide range of climates, including the coniferous and deciduous forests of eastern Russia, the tall grasslands of the Himalayas, and the tropical rainforests of Sumatra and Malaysia (83). Despite the vast territorial range, the tiger population has rapidly declined in recent years. In 1900, as many as 100,000 tigers may have lived in the wild, whereas today, less than 7,000 free ranging wild tigers remain (56, 64, 79). Furthermore, today's free ranging tigers do not live in continuous habitat, but one that has been fragmented into 160 isolated populations scattered across southern and eastern Asia and Russia (Appendix B). Most of these populations are smaller than 120 individuals (32, 56).

Fewer than 3,200 Bengal (79), 400-500 Sumatran (43, 79), 1,200–1,800 Indochinese (79), and 500 Amur tigers are believed to remain in the wild (22, 63, 79). The South China tiger survives as a captive population of 73 individuals managed by Chinese zoos (93).

No definitive estimates predict how many lions remain in Africa. The IUCN Cat Specialist Group concludes there are 30,000-100,000 lions (64). Other estimates, however, are much lower. A 2006 study estimated that there are between 18,000 and

47,000 wild African lions existing today (10). A 2004 study was even bleaker, estimating a wild population of 16,500 to 30,000 African lions (12).

While the African lion is widely distributed in Sub-Saharan Africa (64), the Asiatic lion recently lost a significant portion of its habitat. Historically, the Asiatic lion inhabited a range extending from the coasts of North Africa and northern Greece, across southwest Asia to eastern India. Today, a population of just over 200 individuals remains, confined to the Gir Forest in India (Appendix C) (64). Population sizes of the Sub-Saharan subspecies are unknown.

Captivity

In addition to the wild population of lions and tigers, thousands of individuals live in captivity with an especially well-developed population in the United States. The United States Department of Agriculture (USDA) and the United States Department of Fish and Wildlife (USFWS) oversee this captive population. The USFWS enforces the regulations established by the Convention on International Trade in Exotic Species of Wild Fauna and Flora (CITES). CITES prohibits international commercial trade of tigers and strictly manages breeding and trade for scientific research (24). Fewer restrictions and permitting procedures exist for the lion trade because the African lion is not yet considered an endangered species. The Asiatic lion, due to its highly endangered conservation status, follows the same regulations as the tiger (24). CITES regulations restrict the import of lions and tigers into the United States from abroad, but they have no control over trade within the United States.

The U.S. government has developed regulations to cover areas of domestic trade left unmonitored by CITES regulations. To control domestic trade, the USFWS and the USDA implemented the Lacey Act and the Animal Welfare Act. The Lacey Act prohibits the import, export, transport, acquisition, sale, and purchase of protected exotic wildlife across state boundaries (91). The Captive Wildlife Safety Act, a recent amendment to the Lacey Act, further emphasizes the illegalities in transporting lions,

tigers, leopards, snow leopards, clouded leopards, jaguars, cheetahs, or cougars across state lines (1). USFWS enforces the Lacey Act and its amendments. The USDA enforces the Animal Welfare Act of 1966, which requires any exhibitor or dealer of wild and exotic animals to obtain a permit and undergo USDA facility inspections (3).

Federal regulations enforced by USFWS and the USDA fail to cover trade and ownership within state. In addition, they lack regulations for captive cat ownership outside of dealers and public exhibitors. Furthermore, the federal regulations contain many loopholes. For example, the Captive Wildlife Safety Act does not apply to USDA facilities, allowing frequent interstate trade between USDA licensed exhibitors and dealers (1). Such exemptions make illegal trade easier (91).

In light of these incomplete federal laws, individual states are determining all further regulations on the ownership of lions and tigers in captivity. Different states maintain a full spectrum of regulations. Twenty states permit private ownership of lions and tigers as "pets" (Appendix D). Several, including Alabama and South Carolina, have no laws beyond the federal regulations. In the remaining 30 states, residents cannot legally own lions and tigers as pets. Regulations vary in these states. Some permit captive ownership in AZA zoos only (Washington) and others legalize ownership in USDA facilities, research centers, sanctuaries, government agencies, and nature centers (Connecticut). Several of these states only recently banned private ownership, so individuals owning lions and tigers prior to the passage of the legislation kept their cats. These owners can privately handle the exotic cats they presently own, but they cannot breed them or purchase new felines (Appendix D).

Under past and present international, federal, and state legislation, a large population of lions and tigers developed in the United States. Owners breed these cats for public education, research, entertainment, and companionship. Some owners hope that this captive population can assist in conservation efforts to preserve the wild populations of lions and tigers. In this paper, I present an in-depth study of several facilities handling lions and tigers, including the Association of Zoos and Aquariums, The Institute for

Greatly Endangered and Rare Species, and four exotic cat sanctuaries. I include information about the private realm of captive ownership, but was inhibited by a lack of existing information on privately owned captive lions and tigers. The paper aims to present, in an unbiased manner, the varied practices and attitudes of the animal handlers at each of these exotic cat facilities in reference to how they approach wildlife conservation. My research addresses both the captive rearing methods intended to benefit wildlife conservation, as well as, the multiple flaws in present day management strategies. In the final chapters, I bring all the different practices together to discuss the link between captivity and conservation, to display the lack of collaboration and inconsistent philosophies on the best handling practices, and to demonstrate the need for scientific research about how the thousands of captive lions and tigers in the United States can best help their threatened wild counterparts.

METHODS

I initiated my study of the captive populations of *Panthera leo* and *P. tigris* in the United States by surveying the diverse pool of captive caretakers, inluding zoos, private owners, sanctuaries, research facilities, animal trainers, and circuses. In each survey, I asked the caretaker how many pantherine cats he owned, where he acquired his cats, what methods he practiced in breeding, how he used his captive felines in public education and biological research, and how many generations removed each cat is from its wild ancestors. I sent the survey to 55 zoos affiliated with the Association of Zoos and Aquariums, 23 independent zoos, 10 exotic cat sanctuaries, four circuses, two Hollywood trainers, and one company involved in transporting lions and tigers between captive facilities. Out of these 95 surveys, 18 were returned. I received 11 responses from AZA zoos, two from independent zoos, three from sanctuaries, two from circuses, and none from the Hollywood trainers or the transportation company. The response rate was low at 18%, and few responses included complete surveys.

Because of the low response rate, I turned to a different method to gather information on the captive populations of lions and tigers in the United States. The returned surveys indicated which sources might willingly provide information. Rather than examining data from a large number of facilities, I decided to focus my research on a narrower group of exotic cat owners in greater depth. I became a member of the Association of Zoos and Aquariums (AZA), which provided access to the birth, death, and reproductive records of every AZA lion and tiger. I also joined the Feline Conservation Federation, which put me in contact with private owners, zoos unaffiliated with the AZA, and sanctuaries. With the help of these contacts, I undertook case studies on zoos affiliated with the AZA, a privately owned large cat preservation center (The Institute for Greatly Endangered and Rare Species), and four large cat sanctuaries.

Through email, telephone interviews, and some site visits, I studied how these captive localities facilitate conservation of the lion and tiger in the wild, assuming that using responsibly managed captive cats in biological research and public education is beneficial

to conservation. The study of each facility was two-part. First, I studied the individual lions and tigers. When available, I gathered medical records indicating individual health, age, life span, reproductive success, distance to wild ancestry, and subspecies purity. I also researched the number of pantherine cats in each facility and, in cases where the caretakers practiced controlled breeding, the breeding methods. Second, I asked the owners about their purpose for keeping pantherine cats in captivity, their opinions on maintaining subspecies and species diversity, and the ways in which they use exotic cats for public education and biological research.

In addition to interviewing captive caretakers, I contacted the United States Department of Agriculture and the state branches of the Department of Fish and Wildlife. From these government contacts, I learned about federal and state laws as well as the number of facilities licensed, by both the federal and each state's government, to hold exotic cats in captivity.

I combined the information collected from captive owners and the government with a review of the scientific literature. I researched the phylogeny of pantherine cats and their historic and current geographic range. In addition, I reviewed articles on the illegal trafficking of exotic cats, the academic debate over maintaining species and subspecies distinctions, the necessity for developing captive population sustainability, and the potential role of captive felines in wildlife conservation.

THE ASSOCIATION OF ZOOS AND AQUARIUMS

With 217 accredited facilities, the Association of Zoos and Aquariums (AZA) is the largest accredited zoological community in the United States (4). Every year, zoos affiliated with the AZA receive over 143 million visitors, more than the combined annual attendance of every professional baseball, basketball, and football game (25, 37). The AZA educates the public on exotic and endangered mammals, birds, reptiles, amphibians and their habitats - educational opportunities unparalleled by any other facility in the United States. Such a large public audience, however, comes with many challenges; the AZA must balance entertaining and educating the public with the interests and welfare of the animals themselves. Many of these animals have rapidly declining populations in the wild. The AZA strives to work with the captive population to increase the chance of survival of wild populations.

The mission statement of the AZA declares that its member zoos are devoted to "excellence in animal care and welfare, conservation, education, and research that collectively inspire respect for animals and nature" (4). I use the captive lion and tiger populations as study species to examine the current efforts of the AZA to balance animal welfare, conservation, education, and research.

Many of the animal welfare concerns that the AZA handles involve unease about the sizes and designs of cage enclosures (60, 62, 73), animal health (27, 34, 73, 81), and breeding practices (25, 76, 81). The AZA aims to alleviate each of these concerns by developing a well-managed, genetically diverse, highly out-bred, and reproductively sound captive population to serve as a hedge against the extinction of these species in the wild (104). Members of the World Zoo and Aquarium Conservation Strategy declare, "To maximize value to conservation, *ex situ* populations need to be demographically stable, well-maintained and capable of self-sustaining reproduction" (71). According to the World Conservation Union, the lack of sufficiently managed captive populations hinders conservation of the Felidae (64). The International Union for the Conservation of Nature (IUCN) expands this idea, claiming that the development of captive species

management programs is a defining characteristic of the zoo's evolution from a menagerie into a conservation center (64).

In order to specifically maintain the captive lion and tiger populations, the AZA has established Taxon Advisory Groups (TAGs) and Species Survival Plans (SSPs). TAGs are created for specific animal groups that the AZA focuses on conserving through efforts to research, manage, and conserve the captive and wild populations in question. The Feline TAG is dedicated to building a stable but small captive population (9). Leslie Field, the lead animal keeper at the Sacramento Zoo, notes that spatial limitations hinder breeding in the AZA. There are just over 200 facilities, many in urban settings, and thousands of species threatened by wild extinction that the AZA would like to support. To efficiently focus their efforts, the AZA Taxon Advisory Groups design SSPs for "flagship species" to arouse strong feelings in the public (8). "Flagship species" enable the AZA to focus their conservation efforts on a manageable population that will attract the curiosity and financial support of the public – support that is necessary for zoos to survive. Both lions and tigers qualify as "flagship species." AZA facilities, Field continues, prioritize the quality of living space for the cats at the expense of the number of cats in each facility. While the Denver Zoological Garden and the Kansas City Zoo have the largest populations, with 10 lions each, the Sacramento Zoo has only five tigers and two lions and the Chicago Zoological Park has a single lion (26, 104).

With each facility holding so few animals, a breeding population is sustained by regional population management. The lion SSP and the tiger SSP manage each of these populations. As of April 2007, there were 133 pedigreed African lions in 40 different North American AZA zoos. There are a total of 141 pedigreed lions in the AZA studbook, but eight of these individuals presently live in South African zoos, leaving 133 individuals in the United States (74) (See Appendix E for age distribution). An AZA studbook deems an individual as pedigreed when it has known genetic ancestry. The Felid Taxon Advisory Group set the target population size for the pedigreed African lion at 350 individuals (26). Currently, nearly 300 pedigreed and non-pedigreed 'generic' lions reside in AZA facilities. Generic lions are frequently rescued from other facilities

and are either of unknown ancestry or of hybrid descent between different *Panthera leo* subspecies (26). These lions are not included in the breeding population and do not contribute to the target population size.

Every pedigreed lion managed under the SSP is of a known origin, has wild ancestry that goes back to southern Africa, and is of the subspecies *Panthera leo krugeri.* Today's captive population in AZA accredited zoos descends from 48 founder individuals (74) and is believed to maintain 97.5% wild genetic diversity (26). Hollie Colahan, head of the lion SSP, believes there is no longer any need to introduce wild lions into the captive gene pool for genetic enrichment because of the high percentage of wild genetic diversity in the captive lion population (102). The 48 founders of the AZA lion population were either captured in the wild or born in captivity from two wild-born parents. Only 30 of the 48 founders entered AZA facilities. Founder individuals with studbook numbers 15 through 20 all come from Bulawayo, Zimbabwe. Despite being listed as founders, none of these lions ever entered the AZA, but instead were bred in captivity in Zimbabwe and have offspring that came to the AZA zoos. The AZA does not have birth or death records of these animals. They only know of the animals' wild birth and subspecies distinction as *Panthera leo krugeri* (See Appendix F) (26).

The AZA SSP does not manage any other lion subspecies. In 1981, the AZA established a SSP for the Asiatic lion to manage a population of over 200 individuals living in Australia, Asia, Europe, and North America. This was the only population of Asiatic lions outside of India and was believed to originate from a founder population of seven individuals. In 1987, however, research unveiled that this population was of hybrid Asiatic and African lion descent (66). The Asiatic lion SSP run by the AZA ended because there was not enough purity to build an effective captive program. In the mid-1990s, the European Breeding Programme (EEP) began a new Asiatic lion SSP that continues today (102).

The SSP manages the AZA lion population through the *Panthera leo krugeri* studbook, a record of all the births, deaths, and transfers of individual animals. The studbook builds

family lineages, enabling keepers to plan reproductive events. It also provides data on fecundity, survival, and mortality of males and females at each age, which is necessary for the AZA to forecast the population's future stability (Appendix G). Hollie Colahan at the Houston Zoo and Joe Christman at Disney's Animal Kingdom direct the lion SSP. With the assistance of veterinarians, reproductive specialists, researchers, and animal keepers, the SSP matches individuals for reproductive purposes. During mate selection, the SSP looks at multiple factors such as relatedness, animal reproductive age, animal health, and concerns of space in facilities. They will only mate two lions if there is minimal potential of inbreeding and if there is space in an AZA facility to house the parents and the cubs (See Appendix H for data on *Panthera leo krugeri* reproductive success) (104).

The AZA determines the potential of inbreeding and selects mating pairs to maximize genetic diversity by assigning each SSP-managed individual a mean kinship value and a kinship value. The mean kinship value determines how closely related a lion is to all the other lions in the current AZA population. If the individual is highly related, the risk of inbreeding increases. Individuals with a rare genetic makeup, on the other hand, have high breeding value because the genes they carry from the founding population have low representation in the present captive population. The AZA SSP breeds felines with low mean kinship values to increase the captive genetic diversity. The kinship value determines the reproductive potential of the tiger's closest relatives. If the relatives are aged with low reproductive potential, the AZA will likely breed the tiger. Thus, individuals with less prevalent genes in the population and whose relatives have limited reproductive potential are valuable for breeding (26, 87).

Tracing the reproductive history of AZA lions reveals the effort required to breed large felines. Some female lions have given birth to multiple litters fathered by the same male. For example, individual 76 who is currently at the Indiana Zoo was born in the wild in 1992 and captured shortly thereafter. Between 1992 and 1994 she traveled between four different facilities in South Africa before coming to Indianapolis in February 1995. In November 1995, she gave birth to her first litter of four cubs, individuals 85-88. All four

cubs died within eight days of birth. She gave birth again five months later in April of 1996 to three cubs, individuals 89-91. Individual 89 was stillborn, but 90 and 91 still live today in Kansas City and Knoxville, respectively. The same female gave birth to a litter of three in 1998 (individuals 125-127), a litter of one in July 2002 (individual 192), and two litters in 2003. Only one cub, individual 125, of the litter born in 1998, is still alive and is located in Santa Barbara. The single cub born in 2002 died at birth. The first litter in 2003 was of a single cub, individual 193, who was born in January but also died at birth. The second litter, born in July of 2003, was of four cubs. Individuals 194 and 195 died at birth, but individuals 196 and 197 reside today in Norfolk, Virginia, and Milwaukee, respectively. Thus, individual 76 has given birth to a total of 16 cubs in six litters. The same male, individual 75, fathered every cub. He was born in the wild, captured in 1993 in South Africa, and traveled between four different South African facilities before coming to Indianapolis in 1995 (74).

Other female lions have given birth to multiple litters, each fathered by a different male. For example, individual 65 was born in the wild in 1992, came to the United States in 1994, and gave birth to four different litters fathered by three different males between 1995 and 2005. During this period, she was moved between Atlanta, GA, Wichita, KS, and Garden City, KS, and mated with a different male at each zoo (74). Such data shows that AZA animals with breeding potential are well traveled and bred with high frequency.

As with the lion, the AZA manages tigers at the level of subspecies through a Species Survival Plan and a studbook. Ron Tilson at the Minnesota Zoo directs the tiger SSP. Captive caretakers debate whether to manage tigers at the species or subspecies level (25, 67, 74, 100, 110, 114). The AZA believes in managing tigers at the subspecies level to maintain the genetic combinations unique to each subspecies. There are many questions, however, surrounding the distance of divergence between tiger subspecies (46, 51, 56, 64). Without a definitive understanding of the distinctions, the tiger SSP maintains subspecies purity so that future research will be able to clarify subspecies relationships (114).

In 1988, the AZA tiger SSP master plan recommended that AZA zoos maintain 175 Amur, 175 Sumatran, 75-80 Indochinese, and 75-80 Bengal tigers, comprising a population of just over 500 individuals (87). By 1992, however, the AZA held a population of 250 Bengal, 200 Amur, 40 Sumatran, and three Indochinese tigers (25). Maintaining the master plan was not feasible, as the growing population size coupled with a desire to maintain at least 90 % of wild genetic diversity in captivity required a greater number of individuals of each subspecies. As a result, the AZA cut back to only managing three of the five tiger subspecies, the Amur, Bengal, and Sumatran, leaving the Indochinese to be managed by European zoological communities (87) and the South China tiger to be managed in China.

Despite this reduction in the number of subspecies they maintain, the AZA continues its struggle to preserve genetic diversity among the tiger populations. Research discovered that all 250 'Bengal' tigers in AZA zoos were in fact hybrids between Bengal and Amur tigers (25). As a result, the AZA no longer manages the Bengal tiger. Rather, the tiger SSP is building a population of Indochinese tigers. As of July 2008, there were 50 Indochinese tigers in AZA zoos. The population continues to grow with five new wild born founders added to the gene pool in 2003. The AZA continues to manage the Amur tiger, which appears stable at a population of 142 individuals. The Sumatran population has grown slightly since 1992, currently standing at 73 individuals (6). The AZA hopes to manage each of the three subspecies at a population of 150 individuals. As a result of the struggles to build a sizable and stable population of Indochinese and Sumatran tigers and due to space constraints, however, the SSP is considering dropping either the Indochinese or Sumatran tiger from management (6).

To handle spatial limitations, the AZA plans to eliminate the non-pedigreed population of lions and tigers. These animals are never bred. The AZA uses contraception to control mating and breeding (78). Separation of males and females at the first sign of estrus is the easiest, although risky, method of contraception. For reversible contraception, the AZA Wildlife Contraception Center recommends the use of Gonadotropin releasing hormone (GnRH) agonists. GnRH agonists suppress the production of estradiol and

progesterone in females and testosterone in males. The AZA uses reversible contraception when they do not want to interfere with an individual's future breeding potential but want to prevent short-term reproduction. For non-reversible contraception used for animals with no future breeding potential, the AZA prefers ovariectomy and, at times, tubal ligation or vasectomy (26).

The AZA considers the animals it never plans to breed "surplus animals." Surplus animals require the same financial support, space, and care as individuals with greater breeding value. Frequently, the AZA shares these individuals with facilities that are not accredited by the AZA. For example, the Alaska Zoo, although not an AZA zoo, presently holds two surplus Amur tigers from the AZA accredited Rosamond-Gifford Zoo in New York. The AZA does not plan on breeding these tigers, and the Alaska Zoo hopes to keep the animals indefinitely for display and public education (98). Breeding these tigers is not in the plan because the population of Amur tigers in the AZA has reached the desired population size (87). As a result, the AZA does not need to breed every pureblood Amur tiger, but instead focuses on breeding Amur tigers with lower mean kinship values and preserving 'tiger space' in zoos for the other subspecies.

With the help of well-developed SSPs and TAGs, the AZA is building self-sustaining captive populations to support the wild populations. It emphasizes, however, that these captive populations will never replace the wild populations. Rather, the SSPs are intended to support future reintroductions of captive individuals into wild populations that are depressed by a lack of genetic diversity (87). The AZA has not yet participated in any lion or tiger reintroductions. Before reintroductions are feasible, conservationists must address the major issues facing wild populations, namely habitat destruction and poaching (114).

In addition to assisting wildlife conservation through the development of stable captive populations and perhaps through future reintroductions, Pukazenthi emphasizes that AZA facilities aid conservation through three other major activities: 1) Public education; 2) Using the captive populations for fund-raising to support research and habitat restoration

in range countries; and 3) Understanding the species through research (114). The AZA visitor impact study published in 2007 assesses the impact of the AZA facilities on public education. Twelve AZA facilities and 5,500 visitors took part in the study. The study measured each visitor's attitude toward conservation, desire to encourage change, and response to the facility's promotion of conservation. The results of the study found that zoos and aquariums play a significant role in conservation education and that visitors believe they gain a stronger connection with nature as a result of their visits (37).

The AZA makes direct efforts to educate the public. Zoo New England, comprised of the Franklin Park Zoo in Boston, MA, and the Stone Zoo in Stoneham, MA, holds sleepovers for groups of up to 25 individuals. They also offer programs for school groups teaching subjects including biodiversity, animal adaptation, habitat, life cycles, the web of life, and careers in wildlife (97). The Houston Zoo runs Camp Zoofari, "an action-packed, hands-on, week-long day camp for kids ages four – twelve." The camp offers the opportunity to learn about the natural world, wildlife conservation, and all of the animals at the Houston Zoo (47).

In return for the unique educational opportunities, the public provides the AZA with the funding necessary for ex situ (outside a species native habitat) and in situ (within a species native habitat) conservation efforts. Between 2001 and 2006, the AZA funded 3,693 conservation projects in over 100 countries, spending an average of 70 million dollars each year. In 2006 alone, the AZA was involved in the South China Tiger Conservation Program in China, the Sumatran Tiger Conservation Program in Indonesia, the Siberian Tiger Conservation Program in Russia, and the Save the Tiger Fund in Asia. Besides field conservation, funding from the AZA also supports research on the lion and the tiger. For example, the Birmingham Zoo, Montgomery Zoo, and San Diego Wild Animal Park have joined forces to investigate the diagnosis of and immunity to the feline coronavirus in non-domestic felines. The Lee Richardson Zoo, the NZP Conservation and Research Center, the Smithsonian National Zoological Park, and The Wilds in Ohio study the estrous cycle, pregnancy, and seasonal patterns in the lion as well as collect African lion testes for reproductive studies and sperm banking (5). Active

representatives of the AZA such as Ron Tilson of the Tiger SSP and Kathy Traylor-Holzer, studbook keeper for the North American AZA tiger population, have both taken part in numerous research initiatives on *Panthera*, studying population genetics and phylogenetic history. The AZA funds in situ research, performs ex situ research, and is comprised of members who are involved in modern day scientific research on both the captive and wild populations of *Panthera.*

The United States government supports the AZA's efforts for population management, conservation, and public education. To further its goals, the AZA collaborates with the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS), the Food and Drug Administration (FDA), the United States Fish and Wildlife Services (USFWS), and the Environmental Protection Agency (EPA). The AZA Governmental Affairs program represents the AZA as a science-based contributor to federal and state legislation on wildlife and conservation (72). In 2005, the AZA collaborated with federal officials, amending the Captive Wildlife Safety Act (1). Conversation with John Goldberg and Pete Thomson of the House Committee on Agriculture revealed that though the federal government works to further captive wildlife legislation, it does not want to hinder the work of the AZA (107). As representatives of the House Committee on Agriculture, they displayed support for the mission, goals, actions, and breeding practices of Association of Zoos and Aquariums.

THE FELINE CONSERVATION FEDERATION

The Feline Conservation Federation (FCF) is a not-for-profit organization dedicated to non-domestic felines and independent of the AZA. The FCF membership is comprised of individuals who own any cat of the 37 species of non-domestic felines in addition to researchers, educators, and commercial exhibitors that are not affiliated with the AZA. Some AZA affiliates are also members of the FCF. FCF members own felines from four pounds to as much as 900 pounds and work with one cat or over 100 cats. The FCF strives to serve the interests of diverse affiliates through a bimonthly journal, husbandry courses, an annual national convention, a board of officers, and an online forum. Through such efforts, it promotes rigid standards for captive facility design and condition, provides a forum through which captive caretakers can share experiences and knowledge, and funds in situ and ex situ feline research. Despite its great diversity, the FCF membership unites in a belief that well-managed captive cats aid conservation (110, 100, 118, 119).

As an organization, the FCF defines and teaches animal welfare standards through feline husbandry courses. Though not required for affiliated FCF facilities, husbandry courses are available and recommended to both member and non-member feline handlers. Each eight-hour husbandry course covers a wide range of topics from federal and state regulations and permitting procedures to public, personal, and feline safety (40). While not species-specific, the information presented is considered to be applicable to animal care for all felines (42). Through husbandry courses, the FCF trains its members to satisfy legal requirements and the highest safety standards, and to raise healthy animals.

As with the Association of Zoos and Aquariums, the Feline Conservation Federation promotes captive feline welfare through an accreditation procedure. Membership to the FCF does not require accreditation, which certifies that facilities are sufficiently large, up to FCF safety standards, appropriately licensed, and that the animals receive proper veterinary care. Licensed veterinarians fill out a facility inspection form and video record the enclosures with the captive felines prior to accreditation. The five-member board of

the FCF accreditation committee approves the facility based upon the results of the inspection. Once accredited, the FCF ensures that facilities maintain standards by requiring an annual report from each facility and accreditation renewal every two years. Accreditation costs $60 initially and upon renewal every two years (41).

In addition to encouraging practices that enhance captive animal welfare, the FCF promotes feline conservation through ex-situ and in-situ research. As an organization, the FCF accepts that the "survival of a species is best achieved in the wild" (39) and that conservationists should prioritize preserving wild habitat for sustainable feline populations. Today, when fragmented habitats, limited population sizes, and politics limit conservation progress in the wild, the FCF relies on captive management and research to help promote the survival of wild species. Thus, the FCF encourages funding field research and supports captive rehabilitation, research, and management programs (39). Dr. Jim Sanderson oversees the allocation of FCF funding for research and wild conservation. Dr. Sanderson is an active member of the International Union for the Conservation of Nature (IUCN) Cat Specialist Group, a group of research scientists who study the population status of wild feline species. His personal research focuses on small and lesser-known wild felines (119), but as a member of the IUCN, he provides objective scientific information on biodiversity, habitats, and ecosystems to identify which actions require highest priority for conservation and to wisely allocate FCF funds (64).

Husbandry courses and accreditation with the FCF are voluntary. As a result, the body of over 560 member facilities holds a wide range of practices and opinions related to feline conservation. The records are incomplete, but there are currently 175 facilities registered to hold 2,095 wild felines (103). There are 613 tigers registered with 39 FCF owners and 201 lions registered with 26 owners. There are also ten ligers (a hybrid between a male lion and a female tiger) registered by four handlers (30). With respect to the mission of the FCF, the majority of members are dedicated to feline conservation through enhancing animal welfare and funding in situ programs. There is no system, however, to ensure a consistency in members' definitions of animal welfare and well-managed populations. There are a variety of captive breeding and rearing practices and a range of beliefs

supporting why these carnivores should be raised in captivity for conservation purposes. Within the FCF and the greater community concerned with animal welfare, such debates are especially fervent in reference to the captive rearing of the charismatic mega fauna, especially the lion and the tiger. Bhagavan Antle of The Institute for Greatly Endangered and Rare Species (TIGERS) and Brian Werner of The Tiger Missing Link Foundation exemplify the variety of breeding and conservation practices of dedicated FCF members.

The Institute for Greatly Endangered and Rare Species

Bhagavan Antle of TIGERS is an active member of the Feline Conservation Federation. He presently sits on the FCF's five-member accreditation panel and hosted the 2008 FCF annual national convention at his facility in Myrtle Beach, South Carolina. He handles 67 tigers, two lions, and four ligers in his Myrtle Beach facility and in the Wild Encounters Program at Parrot Jungle Island in Miami, Florida (100).

Bhagavan Antle works with captive lions and tigers because of his concern over the status of the wild populations. On the telephone, Antle's tone and eager interest reveal his anxiety about the species' survival. He expresses concern about the issues facing wild populations, both in terms of habitat availability and increasing human population density. These issues, which have led Antle to support raising the status of lions to an IUCN species of concern, apply to both lions and tigers (100).

While he expresses interest in both lions and tigers, Antle has dedicated much of his life to working with tigers because he considers them to be the "calling card" of conservation. They are majestic, magnificent, and beautiful, and thus attract public attention (100). With tigers as his mascot for conservation, Antle has dedicated his career to developing a well-managed captive population that will educate and increase awareness among the public on issues of the wild *Panthera* populations and on topics of general biological diversity, ecosystems, and the environment.

Antle has bred tigers for over 25 years, and he estimates that he has bred more tigers than any other individual in the United States. The best practices to ensure healthy and successful captive breeding, according to Antle, are 1) Pairing mates that know one another, 2) Patiently breeding females and providing ample time between litters, 3) Preventing inbreeding, 4) Breeding animals that appeal to the public physically and personality-wise, and 5) Considering the personality and medical history of each tiger prior to mating (105).

Patience is frequently forgotten when breeding in captivity, thus Antle encourages spacing apart multiple litters when breeding a female. Little research exists on wild populations, though records show the interval between litters is a minimum of seven to eight months in cases where a mother lost her previous litter (83). In captivity, Antle believes a female tiger should reproduce with intervals of one to two years between litters. When there are too many cubs in too short a time interval, the mother does not have the resources to care for them, the cubs are small, and their chance of mortality is increased. Antle breeds to maximize litter size and litter health rather than to maximize a mother's frequency of reproduction (101). Not all breeders have the same standards. Due to irresponsible breeding, Antle thinks that the reproductive capacity in captivity is lower than its potential (100).

Further limitations to captive breeding, according to Antle, are the financial costs and space requirements for lion and tiger rearing. He works with 67 tigers and coordinates breeding to provide abundant genetic diversity. Despite the high cost of maintaining each animal, Antle believes that supporting many individuals is necessary to prevent inbreeding and the reproduction of physical maladies and genetic disorders. Unlike the AZA, however, maintaining genetic purity is not Antle's priority. Several years ago, his tigers were genetically tested and the majority was found to be pure Bengal. Since then, Antle has mixed Amur (*P.t. altaica*) blood into the population (101). He is not worried, however, because subspecies distinctions are not his priority. Rather than dwelling on subspecies, Antle focuses on the stability of the generic population, introducing new individuals from other captive facilities whenever his population requires a genetic boost.

Unlike zoos, TIGERS does not transport individuals, breed them, and then continue to move the cats. Rather, when they are in need of new blood in the gene pool, Bhagavan Antle buys tigers from other facilities and these individuals become members of the TIGERS' population (100).

Antle also practices selective breeding by choosing tigers with physical and personality traits that capture the public's attention. Presenting a tiger with dark stripes, deep eyes, and an appealing face enhances a cat's performance ratings in a public show. While almost every tiger cub will attract an audience, their personalities and physical attributes change with maturation, making some tigers more appealing than others. Antle studies the ancestry of each of his tigers to breed the cats with ancestors that were popular among the public. Antle also breeds the felines that are, personality-wise, most receptive to a public audience. Since Antle requires well-behaved tigers for his public displays, a tiger that is cooperative on stage, responsive to a handler, and most easily trained is selectively bred (100).

For public appeal, TIGERS also breeds the white tiger and the golden tabby. White tigers characteristically carry the brown stripes of a standard tiger. In place of the yellow-orange coloring, however, white tigers are whitish-gray. A golden tabby also carries the brown standard stripes, but has white and strawberry blonde pigment in place of the normal yellow-orange coloring. Both the white tiger and the golden tabby are color morphs and not separate subspecies. These color morphs occur because of autosomal recessive alleles. A white tiger must inherit two copies of the recessive allele that is responsible for reduced fur pigmentation (44). Similarly, a golden tabby must carry two copies of the recessive allele responsible for its coat color. White and golden tiger progeny are only guaranteed when two adult white or golden tigers are bred; however, so few color morphs exist that homozygous matings carry high inbreeding potential. Antle disagrees with claims that all captive white and golden tigers are inbred. He breeds color morphs through standard out-breeding (100). When a white tiger is bred with a standard tiger, the color morph alleles remain within the gene pool because each standard colored cub of the F1 generation serves as a heterozygous carrier of the recessive allele

responsible for a white tiger. A member of the F1 generation, when bred with a white tiger, carries a 0.5 chance of producing white tiger progeny. When bred with a standard tiger, a member of the F1 generation will not produce any white tiger progeny, but .25 of the progeny will carry the recessive gene responsible for the white coloring. This practice allows Antle to maintain genetic diversity while preserving the color morph alleles in the population.

Antle believes that breeding color morphs does not hinder the health of individual felines and, in addition, helps promote education. Exhibition for public education is the driving purpose behind Antle's captive tiger, lion, and liger population. His public exhibit is no circus act; it is an informative and biologically accurate dialogue detailing the history and present day conditions of the wild tiger population. When presenting tigers to the public, Antle has found the audience most receptive to animals of unique color morphs and of various ages. If he brings on stage a three-month old golden tabby, a year and a half old golden tabby, and a mature golden tabby, the audience reacts both to the unusual color of the feline, and to the dramatic differences in the sizes of a cub, an adolescent of 200 pounds, and a full grown 500 pound adult. In such a presentation, Antle teaches an attentive public about tiger physiology and maturation.

At TIGERS, Antle also breeds ligers. He produced his first litter of ligers 20 years ago and six years ago produced a second litter. He has found that ligers captivate the public. During his show, Antle waits until the very end to bring a liger onto the stage. As a result, the audience waits in anticipation, paying close attention to the rest of the presentation. A liger is the world's biggest cat, and as Antle states, people are wrapped up in "World's Biggest Anything" (100). The highlight of "The Tiger Stage" at King Richard's Faire is his liger Hercules who weighs 900 pounds and stands at 11 feet from his rear paws to the top of his head. Along with the rest of his breeding practices, Antle breeds the liger because the public is receptive and thus more likely to hear his conservation message.

Antle has three different public displays: one in Myrtle Beach, SC, another in Miami, FL, and a third traveling exhibit that comes to King Richard's Faire in Carver, MA. The Myrtle Beach Tiger Reserve houses Antle's most interactive public exhibit and is designed to serve what Antle believes is the greatest purpose of captive felines: enabling a public audience to see and interact with wildlife so that they will be inspired to assist wild populations. It includes a high-speed track where the general audience watches a tiger chase a lure, reaching speeds of nearly 50 miles per hour. In addition, TIGERS has a glassed-in swimming pool where an audience can see tigers play, swim, and interact with trainers. The most popular aspect of the Myrtle Beach facility is the only one that costs money: a tiger photo booth where families and small groups can have photographs taken with tiger cubs. Antle estimates that the exhibits at the Myrtle Beach venue receive over three million visitors each year. To Antle, that translates into three million people each year learning about and gaining respect for the wild tiger (101). Profits from the photo booth and gift shop support the upkeep of the facility and its animals, as well as wild conservation efforts. TIGERS currently supports a development project in Thailand building educational centers to increase local awareness, inspire habitat protection, and reduce poaching (100).

At Parrot Jungle Island and the King Richard's Faire, TIGERS presents the Tale of the Tiger Show, which is an informative presentation of the felines outside of cages. The Parrot Jungle Island performance has an average annual attendance of between 300,000 and 350,000 people; the King Richard's Faire, a seasonal showing, reaches a total audience of 100,000 to 150,000 people each year (101). During the Tale of the Tiger, Antle and the trainers bring the golden tabby, white tigers, grown tigers, young tigers, and ligers onto the stage. The trainers hold the felines by a chain leash and feed bottled milk to the cats as a treat while they are onstage. As the audience watches, Antle talks about the animals' wild habitats and basic life histories.

In the past, Antle has reached an even greater public audience through a more extensive traveling presentation. When he began traveling performances about 25 years ago, Antle found that Renaissance Fairs typically hosted an environmentally aware and receptive

audience. He also found that the owners and organizers of the fairs shared similar political views to his own and were enthusiastic about the Tale of the Tiger show (100).

The owner of the King Richard's Faire was in attendance at one of Antle's performances and offered to build a stage and a living space for TIGERS in Carver, Massachusetts. At the back corner of the faire grounds is a small pen where two tiger cubs play behind a chain link fence. The cubs climb on top of and hide behind a small wooden box. They chase balls and chew upon them, and occasionally they pounce on each other. On the opposite side of the fence, a diverse audience watches them with wide eyes. To the right of this "tiger zoo" is the "tiger stage". Wooden benches that seat several hundred people are lined up in front of the stage, which is set with large crates for the tigers to sit on during the performance. Large doors lead backstage to the living quarters where the animals and trainers reside during the faire season, from Labor Day through October. Due to state and federal laws and advocacy groups, Antle has much less freedom to travel today. The King Richard's Faire, because of its facilities and enthusiastic audience, remains the only Renaissance Faire venue that TIGERS attends.

Through the three venues where he shows his felines, Antle represents the mission of the FCF, promoting conservation, animal welfare, and public education. Despite the support he receives from the FCF, not everyone shares the same respect for Antle. 911 Animal Abuse, an online forum, criticizes Antle and his facilities. To the public, Antle is frequently known as Doc Antle because he is a doctor of Medicine (38). 911 Animal Abuse believes 'doctor' is a misleading title, reporting that Antle earned a doctor of natural sciences degree from the Chinese Science Foundation. In further criticism of Antle, 911 Animal Abuse claims he has multiple aliases including Bhagavan Antle, Kevin Antle, Kevin Bhagavan, and Mahamayavi Bhagavan Antle. It also claims that he runs a mobile petting zoo, criticizes him for leasing tigers for TV commercials and movies, and states that "Antle hauls around a crossbred lion and tiger to such places as casinos" (2).

It is difficult to distinguish exaggerations and misunderstandings from the truth. Antle however, does not hide the criticism he receives (101). In July, 2008, TRAFFIC, the wildlife trade-monitoring network supported by the World Wildlife Fund, visited Antle's presentation at Parrot Jungle Island in Miami. In its report, TRAFFIC criticizes the exhibits of white tigers, golden tabbies, and ligers. TRAFFIC claims that little connection exists between the commercial display of white tiger cubs and wild tiger conservation (91). Antle feels otherwise. TRAFFIC also questions Antle's practices because he does not preserve subspecies distinctions. Furthermore, the report expresses doubts about Antle's claims that his funds support in situ conservation efforts in Asia and questions whether some of his tigers enter the illegal market (91). The report does not provide concrete evidence for these claims, but they do raise unanswered questions.

Debi Willoughby, a member of the Feline Conservation Federation whom Dr. Jim Sanderson speaks very highly of (115), acknowledges that there are many good and bad feline handlers in the United States. Willoughby knows that within both zoos and private facilities, "there are all kinds of people doing all kinds of things" as they breed, rear, and handle endangered felines. Willoughby fully supports Antle and TIGERS, reasoning that Antle has had big cats for many years, is experienced in breeding, works toward conservation with his cats, and is a great resource for learning about how captive lions and tigers aid wild conservation (119).

The Tiger Missing Link Foundation

Brian Werner, another active member of the FCF who is dedicated to tigers, takes a dramatically different approach to conservation than Bhagavan Antle. The founder and director of the Tiger Missing Link Foundation, Werner advocates that captive felines are necessary for the conservation of tigers to serve as a genetic reservoir. While Werner also practices conservation through captive animal education, he prioritizes genetic stability. Founded in 1995, the Tiger Missing Link Foundation is dedicated to preserving the genetic diversity of the tiger, which Werner fears is no longer possible in the wild. He respects wildlife groups that are committed to saving species in the wild and against

captivity but sees that, despite their efforts, wild populations continue to decline, decreasing the genetic diversity within wild populations. In light of such groups' lack of success, Werner fears that wild conservation efforts alone are not enough (118).

The mission of the Tiger Missing Link Foundation is to provide leadership, management, and organization to ex situ tiger conservation through conservation genetics (86). Werner advocates DNA testing as necessary for management of the captive tiger population and for the survival of the species. DNA testing indicates the extent of genetic admixture and diversity and enables future management practices to maximally reduce inbreeding depression, maintain genetic diversity, and maintain subspecies purity (57). DNA testing could provide the information necessary to build a nationwide management program for the breeding of every genetically identified tiger. Werner views this management of diversity as the best way to aid conservation.

Werner hopes that there is a great deal of purity within the captive tiger population in the United States today. His hopes are supported by a recent study by Luo et al. (2008) (57). The study characterized the subspecies genetic ancestry of 105 captive tigers. The researchers identified DNA haplotypes in the captive population that have not been found in the wild population. Furthermore, 49 of the 105 tigers were identified as purebred. A disproportionate number of the tested tigers were in management breeding programs (43 out of 105), but 14 of the remaining 62 tigers were deemed pure (57). Further testing is needed, but these results indicate that there may be genetic diversity in captivity that no longer exists in the wild and that the pool of purebred captive tigers is greater than originally thought. A large population of purebred animals makes building a sustainable genetically managed population feasible. The AZA has already attempted to build such a population, but is limited by space and numbers. There may be cats outside of the AZA but in captivity that could boost the population.

Because of the potential for success, Werner is frustrated that genetic conservation is not practiced today. The Tiger Missing Link Foundation may be the only organization in the United States presently advocating DNA sampling across captive tigers as the only

method of insuring subspecies purity (86). Werner is concerned that little genetic testing has been done to date because of fears that animals in management programs, such as the AZA, are not as pure as breeders thought. Luo et al. (2008) showed that a significant portion of the tigers in managed breeding programs were not purebred (57). Even if these programs have fewer purebred animals than expected, there is still time for genetic testing to begin and breeding programs to change. According to Werner, individual caretakers devoted to the tiger could best serve conservation by genetically testing each cat and entering every purebred cat in the United States into a single management program (118). Werner envisions an ideal captive tiger population, managed through widespread communication and collaboration between caretakers, the government, and the general public (86).

In addition to emphasizing the importance of genetic conservation, the Tiger Missing Link Foundation is the parent organization of a big cat rescue sanctuary known as The Tiger Creek Wildlife Refuge. Brian Werner and a friend, Terri Block, founded the refuge in the late 1990s. Werner supports this facility's potential to promote conservation through public education.

Tiger Creek is a rescue facility for big cats suffering from abuse, neglect or displacement. Tiger Creek is a 25 acre property in East Texas dedicated to helping the ever-growing number of captive big cats in need of a home. Presently, over 30 tigers, three lions, several bobcats, jaguars, leopards, and a puma live at the refuge (84). In addition to acres of natural habitat, the refuge also has what Werner refers to as an 'exercise habitat' with a pool and waterfall for the tigers to play in. Furthermore, Werner is building a veterinary facility with quarantine quarters and a research station. The research station will overlook a three-acre portion of the refuge designed such that the tigers will have little contact with humans. This station will provide opportunities for research on tiger behavior in an environment that simulates the wild. Furthermore, perhaps in the future, the station could help research feasible methods of reintroductions (85).

Werner does not breed his big cats. The Tiger Creek facility's limited space is reserved for animals that need rescue – it does not have room left over for breeding. I do not know how Werner prevents the animals from reproducing.

Werner agrees with Bhagavan Antle that captive tigers are an invaluable resource for public education. In contrast to Antle, however, the Tiger Creek Wildlife Refuge presents rescued tigers instead of selectively breeding tigers to maximize their educational value. Despite their differences, Antle and Werner both advocate for conservation of the tiger through captivity, participate in public education, and promote humane captive caretaking. Their mutual passion and concern for the big cats brought both to the Feline Conservation Federation. Antle hopes that tigers' majestic appeal can boost public interest in environmental education. Werner hopes that the species can be fully preserved in captivity through genetics. Though neither Werner nor Antle focuses on captive lions, their debate and discussion over captive rearing methods will become applicable to lions if they also become endangered in the wild.

EXOTIC ANIMAL SANCTUARIES

Owners frequently prefer captive young lions and tigers to full-grown adults. Nonetheless, every cub eventually develops into a mature feline. With maturity, a cat may outgrow its home, eat more than its keepers can afford, and become too aggressive. A female may also bear more cubs than a facility has space. When such issues arise, owners frequently move their captive cats to exotic animal sanctuaries that are dedicated to "rescue abused, neglected, and unwanted exotic pets and circus animals" (54).

Exotic feline sanctuaries exist throughout North America. Like zoos and other public exhibits, most sanctuaries claim to play an important role in wildlife conservation through education, research, and the promotion of animal welfare. They publicly display live cats to educate the public on the biology and habitats of exotic felines. Sanctuaries are also ample sources of animals for biological and physiological research. Sanctuaries rescue felines from captive mismanagement, uphold animal welfare standards, and promote quality caretaking when they change an animal's living conditions. Sanctuary cats are usually unwanted and neglected exotic pets with unknown ancestries and unknown medical histories, thus making it risky to breed sanctuary cats. In addition, sanctuaries need to spend their resources on rescue efforts rather than on breeding.

Zuzana Kukol of Responsible Exotic Animal Ownership (Rexano), a member of the Feline Conservation Federation, advocates the role of sanctuaries in wildlife conservation. According to Kukol, captive facilities must meet two standards in order to legitimately serve conservation purposes: 1) They must be ethically managed, and 2) They must pursue responsible breeding. Breeding programs stabilize the captive populations of lions and tigers and orient them toward conservation (111). Without captive breeding, captive populations would depend on the capture of wild felines for their sustainability, potentially posing a risk to conservation rather than a benefit.

Despite her call for responsible captive breeding, Kukol advocates that exotic animal sanctuaries not breed. A sanctuary should reserve its limited space and money for

adopting felines that have nowhere else to go (54). According to Kukol, sanctuaries have a more limited role in conservation than other captive facilities because they exist primarily to help animals previously hurt in captivity.

Kukol is not alone in her opinion that exotic animal sanctuaries, especially those serving lions and tigers, should not breed. Lynn Culver, former president of the Feline Conservation Federation, says that sanctuary habitat is not "habitat devoted to species reproduction and continuation" (30). Other realms of captivity may pursue breeding to benefit conservation, but "sanctuaries are transforming themselves into conservation education centers" without breeding (30).

In 1991, Joe Paft founded the Exotic Feline Rescue Center (EFRC) in Center Pointe, Indiana, to provide a permanent home for exotic felines suffering from abuse and abandonment. Set on 108 acres of land, the EFRC provides a home to 191 large cats including 35 lions and 96 tigers, as well as leopards, cougars, ocelots, bobcats, lynx, and a tigon (a hybrid between a male tiger and a female lion). Ten of the tigers were rescued from a traveling circus where they had spent their entire lives living in tiny cages. Another rescue brought King, a nine-year-old male lion, to the EFRC in 2001, when his Minnesota owner could no longer afford to feed him and intended to shoot him and send his body to a taxidermist (35).

Paft agrees with Kukol on the role of sanctuaries in breeding. Mistakes, however, do happen and EFRC felines have successfully reproduced. For example, Paft placed a 14-month-old King in an enclosure with Jasper, an older female lion. The EFRC thought King was too young to reproduce, but when Jasper became pregnant with Lauren a few months later, they learned that King was reproductively mature. Since then both Lauren and Jasper have been spayed (35).

Of the 55 male tigers at EFRC, 22 are neutered and five have vasectomies. Of the 41 female tigers, 27 have been spayed. Of the 11 lions, eight are neutered and the remaining three have vasectomies. Only one of the 24 lionesses has been spayed (108). Animals

either arrive at the EFRC already sterilized or the EFRC sterilizes specific individuals to prevent successful mating. Paft prefers neutering male tigers to spaying the females. When handling lions, an animal that travels in a social pride, Paft prefers to perform vasectomies (113). A vasectomy does not affect sexual behavior (45), thus the lions continue to mate and the sterilization event does not affect a male lion's social status within the pride (113). Though not involved in captive breeding practices, the EFRC serves conservation through its dedication to public education. In 2007, nearly 21,000 visitors toured the facility learning about diet, veterinary care, habitat and behavior (113).

The Conservators' Center in Mebane, North Carolina, which plays an active role in the FCF, also serves conservation through improving captive feline welfare and public education. Like the EFRC, they conduct tours to increase public awareness on issues involving threatened wildlife (29), provide homes for abused and neglected animals, and promote responsible animal care.

Most lions and tigers arrive at the Conservators' Center as a result of USDA seizures. As of January 2009, 12 tigers lived at the Conservators' Center. Eleven of these tigers arrived after USDA licensed facilities failed inspection (30). In 2004, a USDA seizure at a facility in Ohio brought three tigers and 11 lions to the Conservators' Center. Because some females were pregnant, the Conservator's Center had to make room for cubs. In August 2004, the seized tigress Samantha gave birth to four cubs, two of each sex. In addition, 11 lion cubs were born from mothers seized (117).

The center differs from the EFRC and Zuzana Kukol because it does not avoid breeding felines in the sanctuary setting. While the center must focus on rescues, they maintain future breeding potential for some of the felines. They also actively bring in pregnant lions and tigers; as a result, they have practice in rearing cubs. They pull most cubs from their mothers and hand-rear them from about two and a half weeks old. The cubs' caretakers bottle-feed them and monitor each individual's food intake and defecation. Rather than disturbing the cubs through detailed medical check-ups, they determine healthy and unhealthy animals by observing the cubs' daily habits (117). Through their

own responsible rearing, the Conservators' Center strives to educate the public and other captive owners on healthy management of young cubs. It is unclear why the cubs are pulled from their mothers at such a young age.

The Conservators' Center also works toward finding other placements for the felines. For instance, after the destruction and reconstruction of the Baghdad Zoo in 2003, the Conservator's Center donated two tigers from an earlier rescue to support the exhibit space in Baghdad (28). Unlike some sanctuaries that provide permanent homes for rescued felines, the Conservator's Center is often a temporary home. I do not know where the Conservators' Center relocates the majority of its animals.

In addition to public education, sanctuaries also promote conservation through public advocacy. Big Cat Rescue, a sanctuary in Tampa, Florida, supports animal welfare and public education. Built on 45 acres of land and home to 23 different species and subspecies of cats, the facility houses over 200 animals. Although the facility bred felines when it was first founded in 1992, today the founder Carole Baskin avidly speaks against breeding in sanctuaries. Big Cat Rescue seeks resources so that it does not need to turn away the hundreds of exotic cats each year that need a safe home. If the facility bred, its financial and spatial constraints would be even greater (16).

Like Conservators' Center Inc. and the Exotic Feline Rescue Center, Big Cat Rescue devotes its resources to rescues and public education. It differs, however, in its manner of public education. Whereas the Conservators' Center Inc. and the EFRC educate the public through their exhibits, Big Cat Rescue pursues public education without exhibiting cats. Rather, it teaches the public about the plight of captive exotic cats in hopes of reducing the number of animals requiring sanctuary space (15). Big Cat Rescue is currently working to pass legislation such as Haley's Act, a proposed amendment to the Lacey Act, which would prohibit all private ownership of large exotic felines. Furthermore, the act would prohibit the commercial use of cubs in all facilities except for those affiliated with the AZA. Big Cat Rescue publicizes legislative measures and reports cases of animal abuse for public education. They have appeared on NBC, ABC,

CBS, Dateline NBC, the Discovery Channel, and the History Channel promoting animal welfare and increasing awareness of animal rights violations.

Other sanctuaries do not always support the practices of Big Cat Rescue. Kukol and many other members of the FCF do not support legislative efforts that would restrict the private ownership of big cats. Kukol believes that if the government outlaws private cat ownership, they will drive the species extinct (53). It is difficult to define the role of sanctuaries in lion and tiger conservation, as responsible care of captive felines would erase the need for sanctuaries. Tim Santel of USFWS, however, believes that the Exotic Feline Rescue Center exemplifies an ideal captive big cat facility aiding conservation (116). While working for the USFWS, Santel has followed the big cat industry, investigating the illegal trade of big cats and the exploitation of the animals on the market for their body parts (94). He has seen many facilities and remarks that every captive owner portrays himself as an agent for conservation and believes his own activities are beneficial (116). What counts as true wildlife conservation, however, is much more difficult to define.

PRIVATE OWNERSHIP

The majority of captive lions and tigers for which records are available reside in AZA zoos, large sanctuaries, circuses and non-AZA affiliated zoos licensed by the USDA. Many pantherine cats, however, live in private captive ownership as revealed by the rescue operations of the sanctuaries. Although little data is available detailing private ownership, it is thought to include the largest number of captive exotic felines, with lions and tigers living in private homes, basement cages, and backyard farms.

State records are the only indicators of the size of the privately owned captive population. In 30 states, state records indicate the number of privately owned lions and tigers legally within the state boundaries. In the majority of these states, private ownership is illegal, so there are no licensed exotic felines in private ownership. In all the other states with available records, there are very few licensed lions and tigers in private ownership. In most of the states where private ownership is legal, either records are issued on a county rather than state basis and thus unavailable, or I was unable to access them. California requires permits for all facilities not licensed by the USDA. The California Department of Fish and Game has records on the number of people licensed to handle lions and tigers in private facilities but did not grant me access to the records. Similarly, in Texas, where there are thought to be many lions and tigers in private ownership, permits are issued by the county and difficult to compile.

Most of the information available on privately owned lions and tigers comes from investigations spurred by animal welfare concerns. Dr. Tom French of Massachusetts Fish and Game has investigated cases involving the private ownership of pantherine cats in the Bay State. Private ownership of large exotic cats has not been legal in Massachusetts since 1985 (59). Exotic felines are only permitted in large zoos and two visiting exhibits, one presented by Barnum and Bailey's Circus and the other by TIGERS at the King Richard's Faire (105).

French has worked on many cases involving the illegal ownership of exotic cats. Since 1985, investigations in Massachusetts have involved a mountain lion, a white tiger cub, four snow leopards, five cougars, a Siberian lynx, three Canadian Lynx, seven African servals, five bobcats, one African jungle cat, and two Asian leopards (105). While recently investigating a case involving the illegal housing of a mountain lion cub by a family in Ludlow, MA, the Department of Fish and Game found the family waiting for the shipment of their next pet, a white tiger cub. Stopping the shipment was impossible since they had nowhere to return the cub. When the cub arrived, they brought it to the Forest Park Zoo in Springfield, MA (105).

Tim Santel of the United States Department of Fish and Wildlife has also investigated concerns about private individuals and captive *Panthera.* In 2001 and 2002, Santel directed Operation Snow Plow, an investigation of the illegal market for tiger body parts in the United States. Santel went undercover for 18 months and took part in numerous transactions involving tigers. Indictments resulting from this investigation involved a total of 19 tigers (94). Santel investigated cases including a March, 1998, massacre of eight tigers at a warehouse in Alsip, Illinois. During his investigations, Santel noted the attitudes of the defendants toward exotic felines and discovered that many private owners do not view captive lions and tigers as prized and endangered species found in the wild. In the 1998 massacre, one defendant pled that he did not violate the Endangered Species Act because the tigers were of mixed breed, and "only purebred tigers are endangered. Generics…are so plentiful in captivity that they are equivalent to cattle" (94).

In addition to investigating the slaughter of tigers, Santel has also investigated privately owned tigers that live in cramped cages in basements and backyards. He has found tigers chained to the walls of drug dealers' homes in place of a guard dog (94). Situations like these investigated by Fish and Wildlife agents are not uncommon. On Christmas Day, 2008, a one–year-old male tiger was found shot dead on the side of I-35 East in Dallas, Texas. The tiger was declawed and wearing a leash. It is assumed to have belonged to a private family that was no longer able to support it (13).

The United States Department of Fish and Wildlife investigates cases involving endangered species, thus investigations of the illegal market do not yet include cases involving lions, which are also privately owned. Czimer Game & Seafood, a restaurant in Homer Glen, Illinois, advertises lion meat as one of its delicacies. A leg roast of African lion costs $15.95 / pound, tenderloins $24.95 / pound, and ribs are a discount at only $9.98 / pound (31). Although selling lion meat is legal, Czimer Game & Seafood was recently investigated for illegally selling tiger meat as lion meat (91).

The origins of privately owned lions and tigers remain questionable. Many exotic animals enter the private market when USDA licensed facilities close and must find homes for the animals (104, 105). In 1996, a big cat collector in Mississippi was convicted of 73 counts of animal cruelty, and her collection of 86 lions, tigers, and bears was put up for sale at a bankruptcy auction (14). Furthermore, many exotic cats enter the public sphere when small zoos run out of space for all their lions and tigers. Breeding is popular at many small public exhibits because cubs attract the public and bring in money. When space becomes an issue for these facilities, the cats frequently end up in the hands of private owners (104).

Lions and tigers can also be purchased on the Internet, from sites such as www.buytigers.com. A full tiger package costs $13,400 and includes a five-month-old female tiger, an ivory collar, and three tiger toys (18). The Exotic Pet Company, an animal dealer based in Texas, also sells tiger cubs on the Internet (36).

The lack of information on the private captive population makes it difficult to identify its role in conservation. Private facilities do not directly use their animals for public education. There is little evidence indicating that these animals are of any benefit to biological research. Not every private owner, however, is careless, reckless, or in violation of animal welfare concerns. Some private owners belong to the Feline Conservation Federation and promote wildlife conservation. For example, Zuzana Kukol, an advocate of sanctuaries and private ownership in conservation, owns one male African lion and two female tigers (112). Although Kukol finds the breeding of captive

cats necessary for conservation (53), she does not breed her animals (112). When I talked with Debi Willoughby of the FCF, whom Dr. Jim Sanderson regards with great respect, she revealed her belief that some private owners have well-founded reasons for owning lions and tigers. In every profession, Willoughby explains, there are good and bad people, and the same holds true for private exotic feline handlers (119).

INCONSISTENCIES AMONG CAPTIVE LION AND TIGER OWNERS

The Association of Zoos and Aquariums, the Feline Conservation Federation, and many exotic wildlife sanctuaries support captive populations of lions and tigers and wildlife conservation. Habitat loss presents one of the greatest threats to wild large cat populations, but rebuilding the necessary habitat for these cats, especially tigers, presently seem daunting (10, 63, 70, 90). With little hope of a sudden resurgence of these wild populations, captivity plays a significant role in the survival of these species. Unfortunately, there are serious flaws in the management of the captive lion and tiger populations in the United States. Research has unveiled the practices of only a few captive feline handlers, yet this small window portrays serious deficiencies in the current system. Such deficiencies include the lack of monitoring and census data tracking the exotic felines in the U.S., disagreements among handlers over breeding practices, inadequate scientific records of captive management methods, and an absence of efforts to determine the best practices for promoting a stable, healthy captive population.

Issues of Monitoring Captive Lions and Tigers:

We have no idea how many captive lions and tigers live in America. A public exhibitor's lion is licensed with the United States Department of Agriculture, a lion in Kansas is registered with the county sheriff, and a tiger in Alabama is unregistered. Problems recur in the absence of a uniform method to register privately owned large cats. In addition, there is no regulation of the captive population, allowing inadequate facilities to house these large cats and exotic animal trafficking to continue.

Without federal regulations or record keeping, many states have developed their own laws to monitor exotic animal handling. State laws vary, prioritizing public safety and showing little concern for animal welfare (91). Many states that require the registration of lions and tigers also regulate the dimensions of the animals' enclosures. In California, the owner of an exotic feline must have an enclosure with 300 square feet of floor space surrounded by an eight-foot fence for each lion or tiger (20). In Maine, lion and tiger

cages only require 150 square feet of floor space surrounded by a six-foot fence (58). The difference – almost half that of California – demonstrates the arbitrariness of state regulations in cage size. Without knowledge or understanding of the animal, regulations consider public safety with little regard to the needs of the animals. Some states have no laws at all regarding big cats, let alone regulations on enclosure size. In such circumstances, nothing prevents a family from keeping a tiger in their living room or in a cage barely large enough for it to turn around.

When facilities are licensed by the USDA or by a state government, they are rarely required to report the purchase, birth, or death of an exotic cat. Thus, unqualified owners can easily acquire exotic animals (91). When a zoo has too many cubs, any individual living in a state with legalized private ownership can bring the kitten home. When the cat becomes too big to handle, some owners shoot it in a garage and sell the body for several thousand dollars with little or no consequence. If law enforcement officers never knew the animal existed, they certainly would not know if the law was violated. Without government documentation of an animal's existence, individuals easily get away with treating animals on the brink of extinction as though they are cattle.

Although the absence of detailed census data elevates concerns for animal welfare, there is scattered and less detailed census data available through the USDA. The USDA has records of all the exotic cats licensed by exhibitors. Unfortunately, the records are incomplete. They record the facilities licensed to exhibit exotic cats but do not specify the species or the number of cats owned (120). Despite the incomplete records, the USDA takes partial responsibility for these facilities, inspecting each one to ensure animal welfare standards and the presence of knowledgeable caretakers. Beyond the actual licensing procedure and these occasional inspections, however, the USDA does not keep thorough documentation of the population. As a result, some USDA facilities suffer from over-breeding, eventually running out of living space and resources for their animals. Due to such situations, even USDA facilities end up contributing to the presence of animals in sanctuaries (116). Already struggling to manage the population of exotic cats, the federal government is not likely to expand its responsibilities.

Disagreement over Breeding Practices

Legal loopholes make animal welfare concerns difficult to tackle. However, many captive caretakers follow the law and consciously practice responsible animal care. My previous discussion of the AZA, FCF, and sanctuaries demonstrates that there is little consensus over how to manage captive populations of lions and tigers even among these handlers. The lack of consensus is especially clear in the varying breeding practices.

Both Zuzana Kukol and Bhagavan Antle find little necessity of maintaining subspecies distinctions in the captive population. Although Kukol promotes responsible breeding, she does not focus on maintaining subspecies distinctions. Rather, she agrees with the theory that there was once a clinal gradient of tigers within a continuous habitat and that human development divided that habitat, prevented wild landscape continuity, isolated populations, and formed what we see today as a subspecies illusion (51, 56). She advocates against preserving such man-made distinctions (111). This argument is countered by recent genetic studies suggesting the divergence between subspecies of the lion and tiger began too long ago to completely result from recent human activity (<10,000 years ago) (56). Remarkable similarities in the mitochondrial DNA of the Amur and Caspian tiger suggest that these species shared a habitat that anthropogenic activity may have divided within the past 10,000 years (33). These data question whether these populations (one extinct) should continue to be considered as distinct subspecies. The period of divergence between all other tiger subspecies, however, is thought to be a product of genetic drift resulting from geographic isolation due to natural barriers and prior to recent human activity (56, 69). Further research is necessary to fully understand the subspecies distinctions in the tiger lineage and the lion lineage. Captive populations could potentially provide the specimens necessary for such research. Research on subspecies distinctions would be beneficial to conservation plans for protecting tiger habitat in the wild (56).

The impact of human activity on tiger subspecies is unresolved, but Kukol may have a point in her claim that the majority of tigers in captivity in the United States today are of

hybrid Bengal / Amur descent. The genetic ancestry of most tigers in captivity outside of AZA facilities is unknown. If the captive population is mostly comprised of hybrid individuals, an idea that has been hypothesized but not genetically proven, perhaps it is most efficient to focus breeding on the captive generic tiger rather than each subspecies. Kukol has coined the hybrid Bengal / Amur cross the 'American tiger.' Through responsible captive breeding of this 'American tiger,' she hopes that we can build a self-sustaining captive population able to eliminate pressure on wild populations. If a well-established captive population is built, it can supply felines for research purposes or to boost a captive gene pool. Kukol further argues that the AZA, with only a handful of animals, does not have enough genetic diversity to maintain subspecies distinctions (111). Antle agrees, arguing that it is important to build a secure population of lions and tigers in the U.S., but that it is unnecessary to worry about subspecies distinctions when it does not seem to be practical in captivity (100).

Kukol and Antle make reasonable claims. Within the AZA, the population of every tiger subspecies consists of less than 150 individuals, the minimum that the tiger SSP believes is necessary to maintain 90 % of the wild tiger genetic diversity far into the future (6). Even if it were possible for the AZA to build a population with sufficient individuals and genetic diversity, it might not have enough space to hold all these tigers. To maintain 150 individuals of three subspecies, the AZA would need space for 450 tigers. As of 2008, the AZA SSP reports that it has only 357 spots available for tigers in AZA zoos (6). Furthermore, 150 individuals might not be adequate for reproductive and genetic stability. Other suggestions recommend a minimum viable population of 175 individuals (25), while others claim that 500 individuals (76) are required to build a stable population.

The AZA, however, does not believe in eliminating subspecies distinctions to solve space limitations. The association maintains subspecies in order to build a "well-managed, genetically diverse, highly outbred, and reproductively sound population" that will maximize the impact of captive populations on conservation (7). The African lion population shows success within the AZA, having a stable population of 133 pedigreed

individuals and an inbreeding coefficient of f = 0.028 (26). The AZA supports its platform by emphasizing the importance of maintaining subspecies distinctions. Many conservationists, who are not necessarily associated with the AZA, argue that for captivity to benefit wildlife conservation, captive breeding requires controlled conditions that maintain subspecies distinctions to preserve biodiversity (67, 76, 79). Joe Paft of the Exotic Feline Rescue Center says facilities that independently breed, are not involved in an SSP, and are unconcerned with subspecies distinctions focus on the immediate health of the population rather than on long-term efforts of conservation (113). He believes that species survival plans at the subspecies level are necessary for the future stability of a population beneficial to conservation. By conserving at the subspecies level in captivity, we not only preserve unique genetic combinations and great genetic diversity among lions and tigers, but we also enable scientists to investigate the distinctions between subspecies and gain a greater understanding of the evolutionary history and present diversity of wild populations (104, 113, 118).

Beyond issues over whether to prioritize subspecies distinctions in captivity, captive breeders suffer further divisions over breeding practices. Bhagavan Antle finds multiple flaws in the AZA breeding practices. Antle advocates for breeding among mates that know each other prior to reproductive attempts. He dislikes the AZA practice of transporting animals across the country to breed with an unknown partner. On the other hand, though unaffiliated, Paft supports the AZA reasoning that transportation does not diminish breeding success (113). Besides heated statements from different captive handlers, no data have been collected on the question whether transportation diminishes lion and tiger reproductive success.

Antle also disagrees with the practice of breeding a single female with high frequency. Some individual lions and tigers in the AZA, such as lion 40 of the *Panthera leo* studbook, are bred again shortly after giving birth. Individual 40 gave birth to a litter of three in September 1995, and a second litter, also of three, in September 1996 (74). Antle worries that when females are mated multiple times in close succession, the mother does not have enough energy and resources to support both litters. Antle tries to get to know

his cats and breeds them for the greatest success. He believes the AZA fails to focus on each cat when they put too much breeding pressure on individuals (101). It is unclear if the AZA is hindered by overbreeding.

Antle and others have many criticisms on the breeding methods of the AZA; by the same token, the AZA lacks confidence in most breeding practices outside of the SSP. They do not trust the genetic purity and diversity of cats not involved in their "controlled" breeding program. Maximizing diversity and restoring genetic purity within subspecies is the AZA's primary breeding concern and without involvement in an SSP, it is difficult for breeders to access enough animals and follow genetic patterns with the amount of care required to truly control captive breeding.

An Absence of Scientific Research Studying the Most Successful Methods for Handling Exotic Cats in Captivity

Life table data help determine the breeding practices that can build genetic diversity and enable a self-sufficient captive population of lions and tigers. The studbook data and species survival plans of the Association of Zoos and Aquariums provide data on all the zoos' animals, including life expectancies, reproductive success, mortality rates, and diseases (Appendix G and H). Few captive handlers provide public or scientific access to similar information. Bhagavan Antle says that he will not publicize any medical or life history information on his cats, not because he wishes to hide anything, but because he fears that regardless of what the medical records indicate, someone will use his data to make false accusations (101).

In addition, genetic data on captive lions and tigers are unavailable. The AZA strives to retain 90% genetic diversity in all three tiger subspecies and in the African lion gene pool. They do not, however, follow genetic diversity through DNA testing; instead, they determine genetic diversity by analyzing the founder population of each lion and tiger subspecies and following the mating patterns since those founders (6, 26). Brian Werner emphasizes the importance of genetic testing to preserve the greatest genetic diversity

among lions and tigers and to determine patterns that distinguish subspecies. Only with genetic data can breeders most efficiently avoid inbreeding, preserve great genetic diversity, and discover the differences between subspecies. Nowhere in the United States do caretakers of captive lions and tigers analyze the individual cat's genetics. Werner believes that breeders do not want to study the genetics because they fear that the animals they thought were purebred may actually be hybrid crosses (118).

Finding primary sources in this study was difficult because people hesitate to share information about the lions and tigers they handle in captivity. Many captive feline handlers fear animal rights activists who disapprove of all captive animals. At times, activists break into facilities and kill the cats because they believe that the animals are better off dead than in confinement (107). Activists constantly push legislation to prohibit and criminalize captive exotic cat ownership. Thus, like Antle, many handlers will not share information on their captive cats even if the data shows successful captive rearing, lest activists manage to use the information against them. Exotic cat handlers share information only with people they trust. Steven Katz published the book Lion Taming in 2005. During his research, he worked with private facilities for over a year to build relationships before he was able to gain a behind-the-scenes view of the facilities and an in-depth examination of their practices (109).

Even without the involvement of animal-rights activists, captive facilities frequently receive negative publicity. Zoos make the news because a lion escaped or a tiger mauled a caretaker. Even in less critical situations, zoos and captive handlers receive criticism about the physiological effects of sedentary captive lifestyles and of captive diets on lions and tigers (34, 75, 81). Evidence shows that captive felines frequently have malformed skulls from dietary limitations or from over-grooming, a nervous habit of captive animals (34, 60, 73). The domesticating effects of captivity on wild animals also raise questions (60, 81). It is unknown if a tiger raised in captivity could ever survive in the wild. These questions turn a critical eye on captive ownership. While captivity may not be the perfect solution to revitalizing threatened wild populations of exotic cats, the many positive aspects of captivity end up forgotten. One survey reply I received instantly assumed that I

was on a quest to ignore the “true love and sacrifice in what we (exotic handlers) do” (99). With such paranoia about animal rights activists, handlers become increasingly hesitant to share information and permit research, complicating the quest to build a genetically diverse and stable captive population.

THE FUTURE OF THE LION AND THE TIGER

In this thesis, I discussed the status of lion and tiger populations, focusing on the captive populations in the United States today and examining them with respect to wild populations. Wild lion and tiger populations do not thrive as they once did. Tigers previously had a large and continuous population ranging through the foothills of the Himalayas and the grasslands, rainforests, and deciduous forests of Asia and Southeast Russia. Today, they live in small, fragmented, isolated populations (32, 56, 64, 79, 83). The African lion has not suffered devastation to the same extent; in fact, estimates continue to predict the wild lion population in Africa to range between 16,500 and 30,000 individuals (12). Still, the lion population is unstable. Populations in western and central Africa have begun to fragment (12). Large fluctuations in population size result from human disturbance, disease, and changes in prey density (23).

This loss of stability accompanies an increasing opportunity for captive populations to develop and promote wildlife conservation. Case studies of the Association of Zoos and Aquariums, The Institute for Greatly Endangered and Rare Species, four exotic cat sanctuaries, and a series of federal investigations within the United States, reveal a wide range of philosophies on the best way to breed captive big cats and manage them to assist in wildlife conservation. During this study, I identified several areas where captivity could improve its role in conservation. In this conclusion, I discuss potential responses to the current status of lions and tigers that could help build a better future for these pantherine cats.

Captive programs do not help to directly conserve populations in the wild. Captive populations provide limited aid to wildlife conservation because of spatial and financial constraints, the difficulty of building a genetically diverse and stable population, the risk of domestication, and the complexity of successful reintroductions of captive animals to the wild (25, 75, 76, 81). Despite these limitations, there is potential for captivity to aid conservation through well-directed efforts (27). Due to the limitations of captivity in assisting conservation, caretakers must take every step to manage captive populations

responsibly for conservation. Through the development of coordinated regional and global breeding efforts (27, 80), the collaboration of caretakers around the world (19), the development of scientific knowledge on species' reproductive behavior and physiology (19, 80), and a responsible allocation of limited financial resources (27), it is possible to build captive lion and tiger populations to help preserve the species long into the future. While flawed, current management strategies have the potential, with some changes, to build a population that benefits the preservation of *Panthera* species in the wild.

In recent history, conservation minded animal caretakers have developed stable captive populations of several non-feline species that have aided wildlife conservation. During the 1960s, Przewalski's horse became extinct in the wild as a result of human persecution and low natural growth rates. After wild extinction, the species still existed in captivity via a population managed through an international studbook. As of 2004, 1,800 horses lived in 175 institutions, composing a single captive herd. Reintroduction efforts enabled this captive population to provide a future for Przewalski's horses in the wild. In 2004, the species was successfully reintroduced to two different sites in its native Mongolian range (80).

The case of Przewalski's horse demonstrates the possibility of reintroducing captive-bred animals to their species' native habitat. Multiple factors enabled the reintroduction of Przewalski's horse, including intrinsic characteristics of the species' biology. Responsible genetic management of the captive population (77, 80) and thorough research of the horses' reproductive physiology also enabled scientists to predict how the species would respond to reintroductions. Scientists considered the genetics, reproductive ability, carrying capacity, and environmental sensitivity of the horse to develop a release regime (80).

Similarly, the Arabian oryx, *Oryx leucoryx,* exemplifies the successful reintroduction of a species to its wild habitat. The oryx became extinct in the wild in the early 1960s but continued to exist within a captive breeding program aimed directly at future reintroductions. The first release of the oryx was in 1982, and by 1994 the wild

population included over 400 individuals. Recent poaching has caused a detrimental decline in this rebuilt wild population (82).

In addition to reintroductions, captive populations assist conservation by providing research specimens for studies to benefit wild populations. Research on the captive Asian elephant has led to diagnostic techniques for elephants suffering from tuberculosis (*Mycobacterium tuberculosis*) and a therapeutic plan for treatment (61). Not only has this research helped build healthier captive populations, but it also provides hope for medical research on animals in the wild.

Ringling Brothers holds the largest, most genetically diverse population of Asian elephants outside of Asia (106). Since its inception in 1992, the breeding program has produced 22 elephants at the Center for Elephant Conservation. Considering the difficulty that zoos face in breeding elephants, the Ringling Brothers program is considered incredibly successful. Researchers worldwide have studied the animals at the Center for Elephant Conservation. Ringling Brothers aids conservation through its sustainable breeding program, public outreach, and research on animal biology, physiology, behavior, and reproduction (106). The center has also successfully contributed to global collaboration in conservation.

Unquestionably, lions and tigers differ from Przewalski's Horse, the oryx, and the Asian elephant. Successful captive programs for these other species do not provide a perfect template for the captive rearing of lions and tigers; carnivorous cats have different needs than elephants and ungulates. Furthermore, reintroducing the oryx and Przewalski's horse occurred because each species had self-sustaining captive populations and suitable wild habitat to return to. In addition, conservationists eliminated factors contributing to the species' initial decline in the wild, and researchers understood the species' foraging habits, wild movement patterns, required home range size, habitat preferences, and shelter requirements (52). This depth of information does not yet exist for tigers and lions, making reintroductions currently unfeasible. The programs for other species do, however, offer hope that well-managed captive populations can assist in wildlife

conservation. Furthermore, reintroductions of the lion and tiger may have future potential. First, conservationists need a stable captive population.

A single, responsibly managed breeding population of lions and tigers could benefit the efforts to conserve the species. Thousands of individuals currently live in captivity in the United States. This significant population likely contains great genetic diversity. Furthermore, a passionate group of caretakers in the U.S. today hopes to assist in conservation efforts for the lion and the tiger. Collaboration could provide a future for the captive populations of both species.

For collaboration to occur, the captive management practices for these species must improve. To enable collaboration, conservationists need to create a census and regulatory system tracking every captive lion and tiger in the United States. USFWS TRAFFIC report suggests regulation through managing breeding practices, restricting the sale and transfer of animals, and standardizing body disposal practices (91). These three steps are feasible. Tightening federal and state laws would lead to the registration of every tiger and lion in the United States under a central agency. Registration would make it easy to track the sale, transfer, birth, and death of every tiger and lion. Establishing a single national database to monitor the captive lion and tiger populations would reduce the number of animals in improper homes and minimize illegal trade.

In addition to a central regulating system, the TRAFFIC report proposes implanting every tiger in the United States with a microchip. The same procedure would help regulate the lion population. The chip would link animals with owners, making illegal trade more difficult. Vets can microchip cubs during a routine visit. Adult lions and tigers must be tranquilized, however, complicating the procedure and increasing the expense. To address this complication, TRAFFIC suggests microchipping all exotic cats when they are tranquilized for any medical treatment. In only a few years, we could microchip nearly all lions and tigers in the United States (91). In order for this law to succeed, the federal and state governments must also strictly enforce regulations to ensure that each

animal receives a microchip and is recorded in the central database, and that no illegal trade continues behind closed doors.

After establishing a program monitoring the population of lions and tigers, conservationists need to develop a sustainable breeding population. Many different captive facilities, including AZA and TIGERS, have independently established breeding populations, but a collaborative effort would boost genetic diversity and provide insight into the best breeding practices. Developing a self-sustaining population requires scientific research. A greater understanding of subspecies distinctions through genetic research will help to guide future breeding practices. A recent scientific endeavor, understanding genetic differences will help further research to clarify subspecies distinctions (56). Furthermore, genetic testing could distinguish individuals of pure subspecies in the U.S. captive population, potentially maximizing out-breeding and making possible breeding protocols to conserve the greatest possible genetic diversity and gene combinations unique to each subspecies.

In addition to improving the efficiency of captive breeding practices, recent research has shown that studying subspecies distinctions could help rebuild populations of tigers in areas where the tiger is extinct today. Genetic research shows few differences between the Amur and extinct Caspian tigers, suggesting a recent (<10,000 years ago) divergence between the two subspecies. Such knowledge encourages the idea that the Amur tiger could thrive if introduced to the habitat previously home to the Caspian tiger (33).

Compiling knowledge on breeding techniques, animal behavior, and successful handling practices would assist in building a well-managed, sustainable population. The establishment of a centralized database tracking all the lions and tigers in the United States, a genetic understanding of the species and subspecies, and collaboration between captive caretakers and breeders would help the lion and tiger populations become established as a single captive breeding population, with animals dispersed among several hundred different collaborative facilities. In the past, successful captive programs have

enabled an analysis of captive rearing practices with the compilation of the knowledge of every scientist and caretaker in the field.

Lions and tigers face an uncertain future both in the wild and in captivity. Conservationists struggle to balance the needs of men and carnivores. Growing human populations force conflict between men and wildlife. Large mammalian carnivores frequently require huge areas of preserved land because of their predatory needs and their limited dispersal abilities across developed land (21). Humans also conflict with large carnivores because of over hunting for meat, fur and trophies, or because of the threat posed by large carnivores living near livestock and children. Although they conflict with human development, large carnivores are frequently a focal species for conservation efforts because as an umbrella species they require large home ranges; protecting the large carnivores preserves sufficient land for all the species that have smaller habitat requirements (21, 79). Seidensticker et al. (1999) emphasize the importance of preserving the tiger in the wild, explaining that "the tiger is more than the charismatic predator: it is a keystone species in its environment. By saving the tiger in the world, we save complex ecosystems and habitats that otherwise would be destroyed in the relentless march of human need and, all too often, greed" (79).

In a society lacking the opportunity to see wild animals in everyday life, zoos allow individuals from inner city and developed America to see more than pigeons and squirrels, to understand biological diversity, and to see the animals on Animal Planet and the Discovery Channel in real life. Captivity educates the public and provides research opportunities. Other captive facilities contribute to conservation by enabling the development of strong and convincing science coupled with opportunities for people around the world to see live animals (79). As we look into the future, we see a continued spread of the human-dominated landscape across every corner of the globe. As rainforests fall and natural habitats dwindle, captive populations of lions, tigers, and thousands of other species continue to develop in the United States. Captivity is willing to lend a hand to in situ and ex situ conservation efforts. In an era in need of such wildlife conservation, we must grab this offered hand. With scientific knowledge, we can

pursue biological and physiological research to gain a greater understanding of wild species. With a central agency managing the captive populations, we can maximize the stability and capacity of captive exotic cats to assist in conservation. With worldwide collaboration, we can preserve and restore wild populations of the magnificent and majestic tigers and lions.

WORK CITED

(1) 108th Congress. 2003. Captive Wildlife Safety Act. Public Law. 108-191. 117 Statute 2871.

(2) 911 Animal Abuse. Bhagavan Antle. http://www.911animalabuse.com/00abusers/bhagavandocantle.htm. (accessed February 3, 2009).

(3) APHIS. 1999. Regulations and licensing under the Animal Welfare Act: Title 9—Animals and Animal Products. http://www.access.gpo.gov/nara/cfr/waisidx_99/9cfrv1_99.html (accessed March 10, 2009).

(4) Association of Zoos and Aquariums. AZA accredited zoos and aquariums. http://www.aza.org/Accreditation/AccreditList/index.html. (accessed January 5, 2009).

(5) Association of Zoos and Aquariums. 2006. *Conservation Impact Report.* Silver Spring, Maryland: The Association of Zoos and Aquariums.

(6) Association of Zoos and Aquariums. 2008. *Minutes, AZA Tiger SSP Meeting.* Toldeo, Ohio: Toledo Zoo.

(7) Association of Zoos and Aquariums. Mission statement. http://www.aza.org/aboutAZA/mission/index.html. (accessed January 5, 2009).

(8) Association of Zoos and Aquariums. Species survival plan program (SSPs). http://www.aza.org/ConScience/ConScienceSSPFact/index.html. (accessed January 6, 2009).

(9) Association of Zoos and Aquariums. Taxon advisory groups (TAGs). http://www.aza.org/conscience/consciencetagfact/index.html. (accessed January 6, 2009).

(10) Barnett, Ross, Yamaguchi, Nobuyuki, Barnes, Ian, and Cooper, Alan. 2006. The origin, current diversity, and future conservation of the modern lion (*Panthera leo*). *Proceedings of the Royal Society.* 273: 2119-2125.

(11) Barnett, R., Yamabuchi, N., Barnes, I. and Cooper, A. 2006. Lost populations and preserving genetic diversity in the lion *Panthera leo:* Implications for its ex situ conservation. *Conservation Genetics*. 7: 507-514.

(12) Bauer, H. and Van Der Merwe, S. 2004. Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx.* 38: 26-31.

(13) Big Cat Rescue. $5000 dollar reward. http://www.bigcatrescue.org/video/b42008/5000Reward.htm. (accessed January 17, 2009).

(14) Big Cat Rescue. Big cat bailout. http://www.bigcatrescue.org/000news/0articlesbybcr/2009BigCatBailout.htm. (accessed January 17, 2009).

(15) Big Cat Rescue. Big Cat Rescue's education program. http://www.bigcatrescue.org/edu/education.htm. (accessed January 17, 2009).

(16) Big Cat Rescue. Big Cat Rescue's vision and mission. http://www.bigcatrescue.org/mission_statement.htm. (accessed January 17, 2009).

(17) Brooks, Daniel R., Mayden, Richard L., and McLennan, Deborah A. 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. *TREE.* 7: 55-59.

(18) Buytigers.com. Buy a tiger online? www.buytigers.com. (accessed January 14, 2009).

(19) Cade, Tom J. 1988. Using science and technology to reestablish species lost in nature. In *Biodiversity.* ed. E.O. Wilson, 279-288. Washington D.C.: National Academy Press.

(20) California Administrative Code. 2005. Minimum facility and caging standards for wild animals housed at permanent facilities. Title 14, Section 671.3.

(21) Carroll, Carlos, Noss, Reed F., and Paquet, Paul C. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain Region. *Ecological Applications.* 11 (4): 961-980.

(22) Carroll, Carlos and Miquelle, Dale G. 2006. Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. *Journal of Applied Ecology.* 43: 1056-1068.

(23) Chardonnet, Ph. 2002. Conservation of the African Lion: Contribution to a status survey. Paris, France: International Foundation for the Conservation of Wildlife.

(24) CITES. 2007. Article II *Fundamental Principles* and Article III *Regulation of trade in specimens of species included in appendix I.* http://www.cites.org/eng/disc/text.shtml#III. (accessed February 26, 2009).

(25) Cohn, Jeffrey P. 1992. Decisions at the zoo: ethics, politics, profit, and animal-rights concerns affect the process of balancing conservation goals and the public interests. *Bioscience.* 42 (9): 654-659.

(26) Colahan, Hollie, Pfaff, Sue, and Christman, Joe. 2008. *Analysis and Breeding Plan: Lion Panthera leo Species Survival Plan.* Idaho Falls: The Association of Zoos and Aquariums.

(27) Conway, William. 1995. Wild and zoo animal interactive management and habitat conservation. *Biodiversity and Conservation.* 4: 573-594.

(28) Conservators' Center, Inc. Conservators' chronicle. http://www.conservatorscenter.org/newsletter.html. (accessed January 17, 2009).

(29) Conservators' Center, Inc. Educational tours. http://www.conservatorscenter.org/educationtours.html. (accessed January 17, 2009).

(30) Culver, Lynn. 2009. What is captive habitat? *The Feline Conservation Federation.* 53 (1): 43-45.

(31) Czimers Game and Sea Foods. Products. http://www.czimers.com/2.html. (accessed February 4, 2009).

(32) Dinerstein, E., Wikramayake, E., Robinson, J., Karanth, V., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Connor, M., Hemley, G., and Bolze, D. 1997. A framework for identifying high priority areas and actions for the conservation of tigers in the wild. Washington, D.C.: World Wildlife Fund.

(33) Driscoll, Carlos A., Yamaguchi, Nobuyuki, Bar-Gal, Gila Kahila, Roca, Alfred L., Luo, Shujin, Macdonald, David W., and O'Brien, Stephen J. 2009. Mitochondrial phylogeography illuminates the origin of the extinct Caspian tiger and its relationship to the Amur tiger. *PLoS ONE.* 4 (1): 1-8.

(34) Duckler, Geordie, L. 1998. An unusual osteological formation in the posterior skulls of captive tigers (*Panthera tigris*). *Zoo Biology.* 17:135-142.
The Exotic Feline Rescue Center. A brief history of the EFRC. http://www.exoticfelinerescuecenter.org/about.html. (accessed January 15, 2009).

(35) Exotic Feline Rescue Center. Cat biographies. http://www.exoticfelinerescuecenter.org/albums/album_image/4679242/1393259.htm. (accessed January 15, 2009).

(36) Exotic Pet Co. Large Mammals. http://www.exoticpetco.com/mammals-lg.html. (accessed January 16, 2009).

(37) Falk, J.H., Reinhard, E.M., Vernon, C.L., Bronnenkant, K., Deans, N.L., and Heimlich, J.E. 2007. *Why zoos & aquariums matter: assessing the impact of a visit.* Silver Spring, MD: Association of Zoos and Aquariums.

(38) Feline Conservation Federation. Committee members. http://www.felineconservation.org/members/organizational.php?page=committee_members. (accessed January 7, 2009).

(39) Feline Conservation Federation. FCF conservation projects. http://www.felineconservation.org/programs_services/conservation_grants.htm. (accessed January 7, 2009).

(40) Feline Conservation Federation. FCF wild feline husbandry course. http://www.felineconservation.org/programs_services/husbandry_courses.htm. (accessed January 5, 2009).

(41) Feline Conservation Federation. Inspection form. http://www.felineconservation.org/members/organizational.php?page=inspection_form. (accessed January 5, 2009).

(42) Fortunato, Joe. 2008. Husbandry Course Review. *Feline Conservation Federation.* 52 (5): 23.

(43) Franklin, Neil, Bastoni, Sriyanto, Siswormartono, Dwiatmo, Manansang, Jansen, and Tilson, Ronald. 1999. Last of the Indonesian tigers: a cause for optimism. In *Riding the Tiger: Tiger conservation in human-dominated landscapes.* ed. John Seidensticker, Sarah Christie and Peter Jackson, 130-137. Cambridge: Cambridge University Press.

(44) Guillery, R.W. and Kass, J.H. 1973. Genetic abnormality of the visual pathways in a "white" tiger. *Science.* 180 (4092): 1287-1289.

(45) Hahn, B. 1977. Surgical description of vasectomy in two lions. *Tieraerztliche Umschau.* 32(2): 59-60.

(46a). Herrington, S.J. 1986. Phylogenetic relationships of the wild cats of the world. Ph.D. thesis. University of Kansas, Lawrence.

(46) Herrington, Sandra J. 1987. Subspecies and the conservation of *Panthera tigris:* Preserving genetic heterogeneity. In *Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species.* ed. Ronald L. Tilson, 51-63. Park Ridge, New Jersey: Noyes Publications.

(47) Houston Zoo. Winter camp. http://www.houstonzoo.org/wintercamp/. (accessed January 5, 2009).

(48) Janczewski, D.N., Modi, W.S., Stephens J.C., and O'Brien, S.J. 1995. Molecular evolution of mitochondrial 12S RNA and cytocrome *b* sequences in the pantherine lineage of Felidae. *Mol. Biol. Evol.* 12: 690-707.

(49) Johnson, W.E. and O'Brien, S.J. 1997. Phylogenetic reconstruction of the Felidae using 12SrRNA and NADH-5 mitochondrial genes. *J. Mol. Evol.* 44: S98-S116.

(50) Karanth, K. Ullas and Stith, Bradley M. 1999. Prey depletion as a critical determinant of tiger population viability. In *Riding the Tiger: Tiger conservation in human-dominated landscapes.* ed. John Seidensticker, Sarah Christie and Peter Jackson, 104-113. Cambridge: Cambridge University Press.

(51) Kitchener, Andrew C. 1999. Tiger distribution, phenotypic variation and conservation issues. In *Riding the Tiger: Tiger conservation in human-dominated landscapes.* ed. John Seidensticker, Sarah Christie, and Peter Jackson, 19-39. Cambridge: Cambridge University Press.

(52) Kleiman, Devra G. 1989. Reintroduction of captive mammals for conservation. *Bioscience.* 39 (3): 152-161.

(53) Kukol, Zuzana. 2006. Is Uncle Sam regulating big cats into extinction? REXANO. <http://www.rexano.org//Uncle%20Sam1.htm> (accessed November 4, 2008).

(54) Kukol, Zuzana. 2008. What is a true exotic animal sanctuary? *The Feline Conservation Federation.* 2 (5): 33-35.

(55) Lister, Adrian M. 2004. The impact of Quaternary ice ages on mammalian evolution. *Philosophical Transactions: Biological Sciences.* 359 (1442): 221-241.

(56) Lou, Shu-Jin, Kim, Jae-Heup, Johnson, Warren E., van der Walt, Joelle, Martenson, Janice, Yuhki, Naoya, Miquelle, Dale G., Uphyrkina, Olga, Goodrich, John M., Quigley, Howard B., Tilson, Ronald, Brady, Gerald, Martelli, Paolo, Subramaniam, Vellayan, McDougal, Charles, Hean, Sun, Huang, Shi-Qiang, Pan, Wnshi, Karanth, Ullas K., Sunquist, Melvin, Smith, James L.D., and O'Brien, Stephen. 2004. Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *PLoS Biology*. 2 (12): 2275-2293.

(57) Luo, Shu-Jin, Johnson, Warren E., Martenson, Janice, Antunes, Agostinho, Martelli, Paolo, Uphyrkina, Olga, Traylor-Holzer, Kathy, Smith, James L.D., and O'Brien, Stephen J. 2008. Subspecies genetic assignments of worldwide captive tigers increase conservation value of captive populations. *Current Biology.* 18: 592-596.

(58) Maine Department of Inland Fisheries and Wildlife. 2004. Regulations for wildlife in captivity. 09-137, Chapter 7.

(59) Massachusetts Division of Fish and Wildlife. 1991. Massachusetts Endangered Species Act Regulations. 321 CMR 10.00

(60) McPhee, M. Elsbeth. 2002. Intact carcasses as enrichment for large felids: effects on on- and off- exhibit behaviors. *Zoo Biology.* 21: 37-47.

(61) Mikota, Susan K., Peddie, Linda, Peddie, James, Isaza, Ramiro, Dunker, Freeland, West, Gary, Lindsay, William, Larsen, R. Scott, Salman, Chatterjee, Delphi, Payeur, Janet, Whipple, Diana, Thoen, Charles, Davis, Donald S., Sedgwick, Charles, Montali, Richard J., Ziccardi, Michael, and Maslow, Joel. 2001. Epidemiology and diagnosis of *Mycobacterium tuberculosis* in captive Asian elephants (*Elephas maximus*). *Journal of Zoo and Wildlife Medicine.* 32 (1): 1-16.

(62) Miller, Alyce and Anuj Shah. 2005. Invented cages: the plight of wild animals in captivity. *Journal of Animal Law.* 1: 23-61.

(63) Miquelle, D.G., Pikunov, D.G., Dunishenko, Y.M., Aramilev, V.V., Nikolaev, I.G., Abramov, V.K., Smirnov, E.N., Salkina, G.Pl, Seryodkin, I.V., Gaponov, V.V., Fomenko, P.V., Litvinov, M.N., Kostyria, A.V., Yudin, V.G., Korkisko, V.G., and Murzin, A.A. 2005. *A survey of Amur (Siberian) Tigers in the Russian Far East, 2004-2005.* Deutschland: World Wildlife Fund, Inc.

(64) Nowell, Kristin, and Jackson, Peter ed. 1996. *Status Survey and Conservation Action Plan: Wild Cats*. Gland, Switzerland: IUCN: The World Conservation Union.

(65) O'Brien, Stephen J., Collier, Glen E., Benveniste, Raoul E., Nash, William G., Newman, Andrea K., Simonson, Janice M., Eichelberger, Mary A., Seal, Ulysses S., Janssen, Donald, Bush, Mitchell, and Wildt, David E. 1987. Setting the molecular clock in Felidae: the great cats, *Panthera.* In *Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species.* ed. Ronald L. Tilson, 10-27. Park Ridge, New Jersey: Noyes Publications.

(66) O'Brien, Stephen J., Joslin, P, Smith III, G.L, Wolfe, R, Schaffer, N., Heath, E., Ott-Joslin, J., Rawal, P.P., Bhattacharjee, K.K., and Martenson, J.S. 1987. Evidence for African origins of founders of the Asiatic lion species survival plan. *Zoo Biology.* 6 (2): 99-116.

(67) O'Brien, Stephen J. 1994. Genetic and phylogenetic analysis of endangered species. *Annu. Rev. Genet.* 28: 467-489.

(68) O'Brien, Stephen J. 1996. Molecular genetics and phylogenetics of the Felidae. In *Status Survey and Conservation Action Plan: Wild Cats.* ed. Kristin Nowell and Peter Jackson, xxiii-xxiv. Gland, Switzerland: IUCN.

(69) O'Brien, Stephen J., Luo, Shu-Jin, Kim, Jae-Heuoup, and Johnson, Warren E. 2005. Molecular genetic analysis reveals six living subspecies of tiger, *Panthera tigris. CAT News.* 42: 6-8.

(70) O'Brien, Timothy G, Kinnaird, Margaret F., and Wibisono, Hariyo T. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation.* 6 (2): 131-139.

(71) Olney, Peter J.S. 2005. *Building a future for wildlife: The world zoo and aquarium conservation strategy.* Bern, Switzerland: WAZA Executive Office.

(72) Olson, Steve. 2007. AZA government affairs: the new congress, AZA and how you can help. *Connect Association of Zoos and Aquariums.* April 2007: 14-16.

(73) O'Regan, Hannah J. and Kitchener, Andrew C. 2005. The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Rev.* 35 (3&4): 215-230.

(74) Pfaff, Sue. 2007. *North American regional African lion studbook Panthera leo.* Columbia, SC: Riverbanks Zoo and Garden.

(75) Pitsko, Leigh Elizabeth. 2003. Wild tigers in captivity: a study of the effects of the captive environment on tiger behavior [masters thesis]. Blacksburg, VA: Virginia Polytechnic Institute and State University.

(76) Rahbek, Carsten. 1993. Captive breeding – a useful tool in the preservation of biodiversity? *Biodiversity and Conservation.* 2: 426-437.

(77) Ryder, Oliver A. 1994. Genetic studies of Przewalski's horse and their impact on conservation. In *Przewalski's Horse: the history and biology of an endangered species.* ed. Boyd, Lee and Houpt, Katherine A,75-92. Albany, New York: State University of New York Press.

(78) Saint Louis Zoo. Contraception recommendations. http://www.stlzoo.org/animals/scienceresearch/contraceptioncenter/contraceptionrecommendatio/. (accessed January 6, 2009).

(79) Seidensticker, John, Christie, Sarah and Jackson, Peter, ed. 1999. *Riding the Tiger: Tiger conservation in human-dominated landscapes.* Cambridge: Cambridge University Press.

(80) Slotta-Bachmary, Leopold, Boegel, Ralf, Kaczensky, Petra, Stauffer, Christian, and Walzer, Christian. 2004. Use of population viability analysis to identify management priorities and success in reintroducing Przewalski's horses to southwestern Mongolia. *Journal of Wildlife Management.* 68 (4): 790-798.

(81) Snyder, Noel F.R., Derrickson, Scott R., Beissinger, Steven R., Wiley, James W., Smith, Thomas B., Toone, William D., and Miller, Brian. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology.* 10 (2): 338-348.

(82) Spalton, J.A., Lawrence, M.W., and Brend, S.A. 1999. Arabian oryx reintroduction in Oman: successes and setbacks. *Oryx.* 33 (2): 168-175.

(83) Sunquist, Mel, Karath, K. Ullas, and Sunquist, Fiona. 1999. Ecology, behaviour and resilience of the tiger and its conservation needs. In *Riding the Tiger: Tiger conservation*

in human-dominated landscapes. ed. John Seidensticker, Sarah Christie and Peter Jackson, 5-18. Cambridge: Cambridge University Press.

(84) Tiger Creek Wildlife Refuge. Tiger theatre: Meet the big cats of Tiger Creek. http://www.tigercreek.org/tigershow.html. (accessed February 4, 2009).

(85) Tiger Creek Wildlife Refuge. The vision for Tiger Creek. http://www.tigercreek.org/tcvision.html. (accessed February 4, 2009).

(86) Tiger Missing Link Foundation. Mission statement. http://www.tigerlink.com/. (accessed February 5, 2009).

(87) Tilson, R., Traylor-Holzer, K., and Brady, G. 1994. Regional and global management of tigers. In *Management and Conservation of Captive Tigers Panthera tigris.* ed. Ronald Tilson, Gerald Brady, Kathy Traylor-Holzer, and Douglas Armstrong, chapter 5. Apple Valley, MN: Minnesota Zoo.

(88) Werdelin, Lars. 1996. The history of felid classification. In *Status Survey and Conservation Action Plan: Wild Cats.* ed. Kristin Nowell and Peter Jackson, xviii-xxiii. Gland, Switzerland: IUCN.

(89) Werner, B. 2005. Distribution, abundance and reproductive biology of captive *Panthera tigris* populations living with the United States of America. *Feline Conservation Federation Magazine*. 49 (2): 24-25.

(90) Wikramanayake, Eric D., Dinerstein Eric, Robinson, John G., Karanth, K. Ullas, Rabinowitz, Alan, Olson, David, Mathew, Thomas, Hedao, Prashant, Hedao, Connor, Melissa, Hemley, Ginette, and Bolze, Dorene. 1999. A framework for identifying high-priority areas for the conservation of tigers in the wild. In *Riding the Tiger: Tiger conservation in human-dominated landscapes.* ed. John Seidensticker, Sarah Christie and Peter Jackson, 255-272. Cambridge: Cambridge University Press.

(91) Williamson, Douglas F. and Henry, Leigh A. 2008. *Paper Tigers? The Role of the U.S. Captive Tiger Population in the Trade in Tiger Parts*. Washington, D.C.: World Wildlife Fund, Inc.

(92) Wozencraft, W.C. 1993. Order Carnivora. In *Mammal species of the world: a taxonomic and geographic reference (second edition).* ed. D.E. Wilson and D.M. Reeder, 286-346. Washington, D.C.: Smithsonian Institution Press.

(93) Xu, Y.C., Fang, S.F., and Li, Z.K. 2007. Sustainability of the South China tiger: implications of inbreeding depression and introgression. *Conservaion Genetics.* 8 (5): 1199-1207.

(94) Yates, Jon and Possley, Maurice. 2003. Operation snowplow: tigers bought, sold and killed on lucrative private market. *International Game Warden.* Spring 2003: 18-25.

(95) Yu, Li, Li, Qiung-wei, Ryder, O.A., and Zhang, Ya-ping. 2004. Phylogenetic relationships within mammalian order Carnivora indicated by sequences of two nuclear DNA genes. *Molecular Phylogenetics and Evolution.* 33: 694-705.

(96) Yu, Li and Zhang, Ya-ping. 2005. Phylogenetic studies of pantherine cats (Felidae) based on multiple genes, with novel application of nuclear B-fibrinogen intron 7 to carnivores. *Molecular Phylogenetics and Evolution*. 35: 483-495.

(97) Zoo New England. School groups. http://www.zoonewengland.org/Page.aspx?pid=261. (accessed January 5, 2009).

Personal Interviews:

(98) Alaska Zoo Representative. Telephone interview. November 5, 2008.

(99) Animal Land Zoological Park. Email interview. October 24, 2008.

(100) Antle, Bhagavan. Telephone interview. October 30, 2008.

(101) Antle, Bhagavan. Telephone interview. November 5, 2008.

(102) Colahan, Hollie. Email interview. November 10, 2008.

(103) Culver, Lynn. Email interview. December 26, 2008.

(104) Field, Leslie. Telephone interview. July 23, 2008.

(105) French, Tom. Telephone Interview. April 14, 2008.

(106) Galvin, Joan. Telephone interview. August 25, 2008.

(107) Goldberg, John and Thomson, Peter. Telephone interview. August 12, 2008.

(108) Hall, Jennifer. Email interview. November 14, 2008.

(109) Katz, Steven. Telephone interview. October 27, 2008.

(110) Kukol, Zuzana. Email interview. October 29, 2008.

(111) Kukol, Zuzana. Email interview. November 2, 2008.

(112) Kukol, Zuzana. Email interview. November 4, 2008.

(113) Paft, Joe. Telephone interview. November 5, 2008.

(114) Pukazhenthi, Budhan. Email interview. November 16, 2008.

(115) Sanderson, Jim. Email interview. August 5, 2008.

(116) Santel, Timothy. Telephone interview. November 4, 2008.

(117) Stinner, Mindy. Personal communication. April 17, 2008.

(118) Werner, Brian. Telephone interview. November 25, 2008.

(119) Willoughby, Debi. Email interview. August 6, 2008.

(120) Woods, Tonya. Personal communication. November 5, 2008.

Appendix A: Suggested phylogenies of *Panthera.*

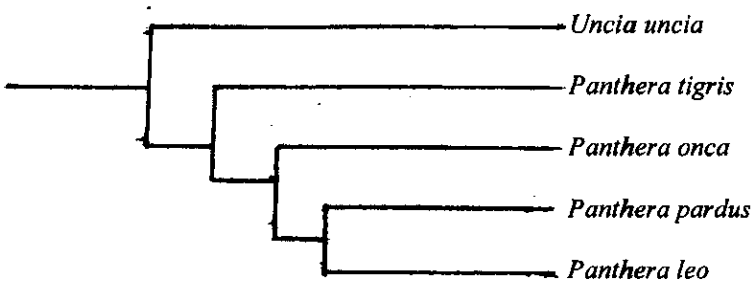


Image 1: Traditional phylogenetic relationships of the *Panthera.* The snow leopard (*Uncia uncia*) is outside the *Panthera* clade. This tree is based upon the phylogeny presented by Herrington (1986) (46a).

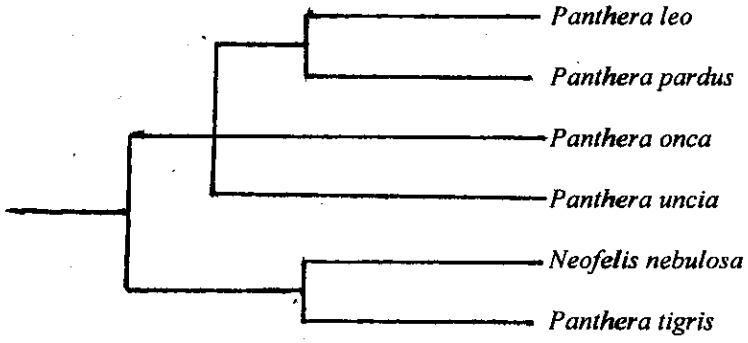


Image 2: Phylogeny including the snow leopard and the clouded leopard (*Neofelis nebulosa*) within *Panthera.* This phylogenetic tree is based on the research of Janczewski et al. (2005) who used molecular analysis from sequences of mitochondrial 12S RNA and the cytochrome b protein coding gene (48).

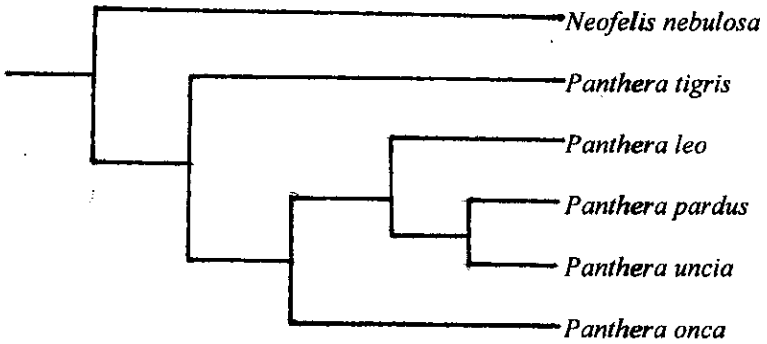
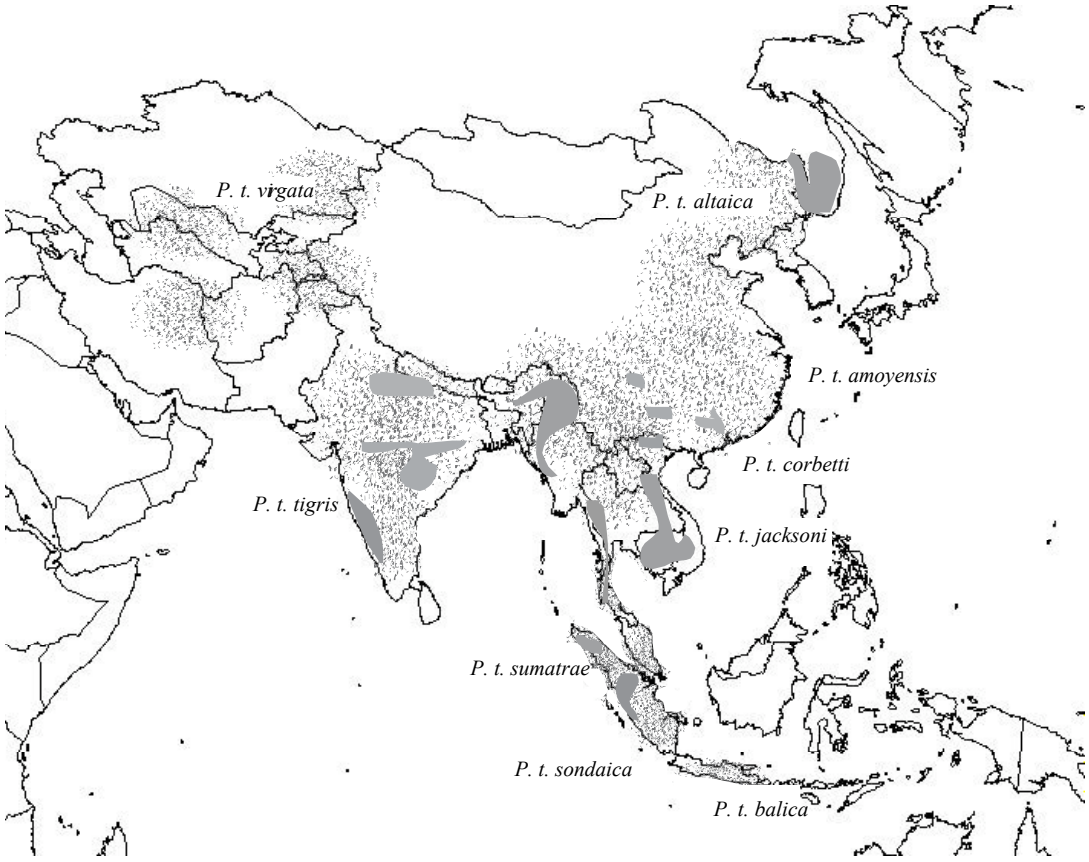


Image 3: The most recent phylogeny developed from a combination of mitochondrial and nuclear DNA by Yu and Zhang (2005) (96). This phylogeny includes the snow leopard within *Panthera* but does not include the clouded leopard.

Appendix B: The historic and present geographic distribution of *Panthera tigris*. The gray dots mark the historic geographic distribution and the solid gray regions indicate the present distribution. The geographic range of each subspecies is also noted. Information for this figure was adapted from Nowell and Jackson, 1996, Kitchener, 1999, and Miquelle et al., 2005 (64, 51, 63).



Appendix C: The historic and present day geographic distribution of the Asiatic and African lion. The gray dotted region beginning in northern Africa and heading east denotes the historic distribution of the Asiatic lion. The gray circle in the Gir Forest, India represents the present day population. The African lion remains in its original habitat throughout Sub-Saharan Africa (marked by gray dots), but the population today is highly fragmented within the region. Information for this figure was compiled from Nowell and Jackson, 1996 and Barnett et al., 2006 (64, 10).

Appendix D:
States allowing private ownership of lions and tigers:
Alabama*
California
Idaho
Indiana
Maine
Mississippi
Missouri
Montana
Nevada
North Carolina*
North Dakota
Ohio*
Oklahoma*
Oregon
Pennsylvania
South Carolina*
South Dakota
Texas
West Virginia*
Wisconsin*

In states marked with an asterisk (*), there is no requirement to license or permit lions and tigers.

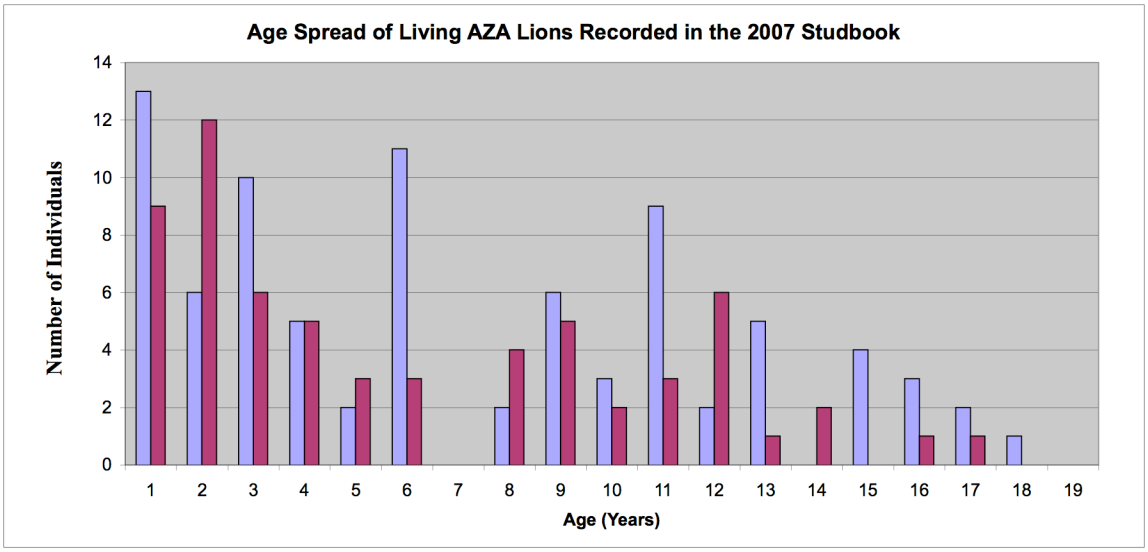
States not allowing private ownership of lions and tigers:
Alaska
Arizona
Arkansas**
Colorado
Connecticut
Delaware
Florida
Georgia
Hawaii
Illinois
Iowa
Kansas**
Kentucky**
Louisiana**
Maryland
Massachusetts
Michigan**
Minnesota**
Nebraska
New Hampshire
New Jersey
New Mexico
New York**
Rhode Island
Tennessee**
Utah
Vermont
Virginia**
Washington**
Wyoming

In states marked with a double asterisk (**), ownership is illegal except when individuals owned animals prior to legislation. These owners are not permitted to breed the animals or acquire new animals.

Information for Appendix D comes from the following sources:

Alabama: Spoke with the Alabama Department of Conservation and Natural Resources. November 4, 2008.
Alaska: Spoke with the Alaska Department of Fish and Game who referred me to Alaska Administrative Code Title 5 Section 92.029. November 4, 2008.
Arizona: Spoke with the Arizona Game and Fish Department. November 4, 2008.
Arkansas: Spoke with the Arkansas Game and Fish Commission. November 4, 2008.
California: Spoke with the California Department of Fish and Game, License and Revenue Branch who referred me to California Codes, Fish and Game Code, Section 2150-2157. November 4, 2008.
Colorado: Spoke with the Colorado Division of Wildlife – Wildlife Conservation. November 4, 2008.
Connecticut: Spoke with the Connecticut Department of Environmental Protection. November 4, 2008.
Delaware: Spoke with the Delaware Department of Agriculture who referred me to Delaware Title 3, Chapter 72, Section 7201. October 31, 2008.
Florida: Spoke with the Florida Wildlife Conservation Commission who referred me to FL Statutes, Title 28 xxviii, chapter 379. November 5, 2008.
Georgia: Spoke with the Georgia Department of Natural Resources. November 3, 2008.
Hawaii: Spoke with the Hawaii Department of Agriculture. November 3, 2008.
Idaho: Spoke with the Idaho Department of Agriculture. November 4, 2008.
Illinois: Spoke with the Illinois Department of Natural Resources who referred me to the Illinois Dangerous Animal Act. November 3, 2008.
Indiana: Spoke with the Indiana Division of Fish and Wildlife. November 3, 2008.
Iowa: Spoke with the Iowa Department of Agriculture. November 3, 2008.
Kansas: Spoke with the Kansas Department of Wildlife and Parks. November 3, 2008.
Kentucky: Spoke with the Kentucky Department of Fish and Wildlife who referred me to 301 KAR 2:082: Transportation and Holding of Exotic Wildlife. November 5, 2008.
Louisiana: Spoke with the Louisiana Department of Wildlife and Fisheries. November 3, 2008.
Maine: Spoke with the Maine Department of Inland Fisheries and Wildlife who referred me to the Department of Inland Fisheries and Wildlife, Chapter 7, Regulations for Wildlife in Captivity. November 3, 2008.
Maryland: Spoke with the Maryland Department of Natural Resources. November 3, 2008.
Massachusetts: Spoke with the Massachusetts Department of Fish and Wildlife. April 14, 2008.
Michigan: Spoke with the Michigan Department of Natural Resources Wildlife Division and Law Enforcement. November 5, 2008.
Minnesota: Spoke with the Minnesota Department of Natural Resources. November 5, 2008.
Mississippi: Spoke with the Mississippi Department of Wildlife, Fisheries, and Parks. November 5, 2008.
Missouri: Spoke with the Missouri Department of Conservation. November 5, 2008.
Montana: Spoke with the Montana Fish, Wildlife, and Parks. November 5, 2008.
Nebraska: Spoke with the Nebraska Game and Parks Commission who referred me to State Statute 37-477.
Nevada: Spoke with the Nevada Department of Wildlife. November 5, 2008.
New Hampshire: Spoke with the New Hampshire Fish and Game Department. November 5, 2008.
New Jersey: Spoke with the New Jersey Division of Fish, Game, and Wildlife who referred me to N.J.A.C. 7:25-4.9. November 12, 2008.
New Mexico: Spoke with the New Mexico Department of Game and Fish who referred me to New Mexico Statutes, Title 19, Chapter 35, Part 7. November 5, 2008.
New York: Spoke with the New York Department of Environmental Conservation. November 4, 2008.
North Carolina: Spoke with the North Carolina Wildlife Resources Commission. November 4, 2008.
North Dakota: Spoke with the North Dakota Board of Animal Health. November 4, 2008.
Ohio: Spoke with the Ohio Department of Agriculture. November 4, 2008.
Oklahoma: Spoke with the Oklahoma Department of Wildlife Conservation. November 4, 2008.
Oregon: Spoke with the Oregon Department of Fish and Wildlife who referred me to the Oregon Administrative Rules 603-011-0710. November 4, 2008.
Pennsylvania: Spoke with the Pennsylvania Game Commission. November 4, 2008.
Rhode Island: Spoke with the Rhode Island Division of Agriculture. November 5, 2008.
South Carolina: Spoke with the South Carolina Department of Natural Resources. November 5, 2008.
South Dakota: Spoke with the South Dakota Animal Industry Board. November 5, 2008.
Tennessee: Spoke with the Tennessee Wildlife Resources Agency. November 5, 2008.
Texas: Spoke with the Texas Parks and Wildlife Department who referred me to Texas Statutes and Codes. Title 10. Chapter 822. Section 101-116. November 5, 2008.
Utah: Spoke with the Utah Division of Wildlife Resources. November 5, 2008.
Vermont: Spoke with the Vermont Department of Fish and Wildlife. November 5, 2008.
Virginia: Spoke with the Virginia Department of Game and Inland Fisheries. November 5, 2008.
Washington: Spoke with the Washington Department of Fish and Wildlife. November 5, 2008.
West Virginia: Spoke with the Virginia Division of Natural Resources. November 5, 2008.
Wisconsin: Spoke with the Wisconsin Department of Natural Resources. November 5, 2008.
Wyoming: Spoke with the Wyoming Game and Fish Department. November 7, 2008.

Appendix E: Age distribution of living *Panthera leo krugeri* in AZA zoos as of April 30, 2007. Blue columns represent the females, and purple columns represent the males. Information adapted from Pfaff, 2007 (74).



Appendix F: The founding population of *Panthera leo krugeri* in AZA facilities. Each of these individuals was born of wild parents. The descendants of these 48 founders are the present day pedigreed individuals in AZA zoos. Many of the founders lived outside of AZA facilities but had offspring that came to the AZA. The dates of birth and death for such individuals are unknown by the AZA (marked as N/A). The number in the column "Founder Individual" is the AZA studbook identification number. The column 'Year of Death' is blank for individuals that were still living as of April 30, 2007. The column 'Number of Years in Captivity' is the number of years from the time the individual was captured until its death or, if it was still living, until April 2007. Information adapted from Pfaff, 2007 (74).

Founder Individual	Sex	Year of capture	Year of Death	Number of Years in captivity
1	M	1965	1977	12
4	F	1972	1977	5
15	M	Unknown	Unknown	N/A
16	F	Unknown	Unknown	N/A
17	F	Unknown	Unknown	N/A
18	M	Unknown	Unknown	N/A
19	F	Unknown	Unknown	N/A
20	M	Unknown	Unknown	N/A
34	F	Unknown	Unknown	N/A
35	F	Unknown	Unknown	N/A
41	M	1989	2003	14
42	F	1989		16
47	F	1990		17
48	M	1990		17
65	F	1992		15
66	F	1993	2003	10
72	M	1976	1997	21
75	M	1993		14
76	F	1992		15
83	F	1997	2003	6
84	M	1993		14
95	F	1995		12
96	M	1995	1998	3
97	F	1996	2003	7
98	M	1994		14
99	F	1980	Unknown	N/A
100	M	1980	Unknown	N/A
101	M	1980	Unknown	N/A
102	F	1980	Unknown	N/A
104	F	1995		12
106	M	1997		10
108	M	1995		12
109	F	1994		13
110	F	1994		13
111	M	1975	Unknown	N/A
112	F	1971	Unknown	N/A
130	M	Unknown	Unknown	N/A
131	F	Unknown	Unknown	N/A
133	M	Unknown	Unknown	N/A
134	F	Unknown	Unknown	N/A
142	M	1996		11
143	F	1996		11
173	M	1995		12
221	M	1995		12
224	F	1996		11
232	F	1997		10
233	F	1997		10
235	F	1998		9

Appendix G: Life table data for males and females of *Panthera leo krugeri* in AZA facilities. Taken directly from Colahan et al., 2008 (26).

	Males					Females				
Age	**Qx**	**Px**	**Lx**	**Mx**	**Vx**	**Qx**	**Px**	**Lx**	**Mx**	**Vx**
0	0.380	0.620	1.000	0.000	1.235	0.310	0.690	1.000	0.000	1.183
1	0.020	0.980	0.620	0.030	1.776	0.010	0.990	0.690	0.010	1.586
2	0.050	0.950	0.608	0.220	1.971	0.030	0.970	0.683	0.220	1.751
3	0.000	1.000	0.577	0.260	1.959	0.000	1.000	0.663	0.330	1.693
4	0.000	1.000	0.577	0.420	1.851	0.020	0.980	0.663	0.300	1.499
5	0.020	0.980	0.577	0.260	1.576	0.060	0.940	0.649	0.340	1.359
6	0.040	0.960	0.566	0.260	1.478	0.000	1.000	0.610	0.150	1.145
7	0.000	1.000	0.543	0.280	1.355	0.050	0.950	0.610	0.290	1.112
8	0.000	1.000	0.543	0.220	1.172	0.030	0.970	0.580	0.280	0.932
9	0.030	0.970	0.543	0.260	1.053	0.030	0.970	0.562	0.190	0.732
10	0.000	1.000	0.527	0.220	0.878	0.030	0.970	0.546	0.240	0.608
11	0.090	0.910	0.527	0.450	0.751	0.000	1.000	0.529	0.040	0.407
12	0.120	0.880	0.479	0.220	0.366	0.000	1.000	0.529	0.400	0.400
13	0.000	1.000	0.422	0.170	0.170	0.000	1.000	0.529	0.000	0.000
14	0.100	0.900	0.422	0.000	0.000	0.070	0.930	0.529	0.000	0.000
15	0.000	1.000	0.380	0.000	0.000	0.080	0.920	0.492	0.000	0.000
16	0.140	0.860	0.380	0.000	0.000	0.000	1.000	0.453	0.000	0.000
17	0.000	1.000	0.326	0.000	0.000	0.000	1.000	0.453	0.000	0.000
18	0.500	0.500	0.326	0.000	0.000	0.250	0.750	0.453	0.000	0.000
19	0.000	1.000	0.163	0.000	0.000	0.000	1.000	0.340	0.000	0.000
20	1.000	0.000	0.163	0.000	0.000	0.500	0.500	0.340	0.000	0.000
21	1.000	0.000	0.000	0.000	0.000	1.000	0.000	0.170	0.000	0.000
22	1.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000

Qx = mortality; Px = survival; Lx = cumulative survivorship; Mx = fecundity; Vx = expected future reproduction

Appendix H:

Table 1: Reproductive output of *Panthera leo krugeri* in AZA facilities. This data is calculated from both the living and deceased individuals recorded in the *Panthera leo krugeri* studbook. Information calculated from Colahan et al., 2008 (26).

Average number of mates / female	1.223
Average number of mates / male	1.595
Maximum number of mates / female	3
Maximum number of mates / male	4
Total number of females mated	49
Total number of males mated	37
Average number of offspring / female	4.408
Average number of offspring / male	5.784
Average number of litters / female	1.857
Maximum number of litters / female	6
Average number of cubs / litter	2.369
Maximum number of cubs / litter	6
Maximum number of offspring / female	16
Maximum number of offspring / male	21

Figure 1: The female lions recorded in the AZA studbook and the number of cubs / litter each lion has given birth to as of April 30, 2007. Different colors indicate different litters. The height of each column represents the number of cubs. Information adapted from Pfaff, 2007 (74).