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MS ENVIRONMENTAL BIOLOGY CAPSTONE PROJECT

by

Shanelle J. Thevarajah

A Project Presented in Partial Fulfillment of the Requirements for the Degree Masters of Science in Environmental Biology

> REGIS UNIVERSITY May, 2021

MS ENVIRONMENTAL BIOLOGY CAPSTONE PROJECT

by

Shanelle J. Thevarajah

has been approved

May, 2021

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CHAPTER 1. LITERATURE REVIEW

Coexistence begins with respect: human impacts on brown bears (Ursus arctos)

Grizzly bear (Ursus arctos) populations have had a troubling history of extirpation, and due to the growing human population, continue to face threats today (Eisenberg, 2014). In 1814, based on accounts of the Lewis and Clark expedition, the grizzly bear was renamed U. horribilis by taxonomist George Ord. This name directly translates to "northern horrible bear," setting a precedent for harmful human relations with this species. In 1975, US Fish & Wildlife Service (USFWS) put grizzly bears on the federal list of endangered plants and animals, under the Endangered Species Act (ESA), to protect their populations from human hunting (Eisenberg, 2014). These hunting practices stemmed from the lack of understanding of large carnivores and were largely driven by human fear. Grizzly bears have been thought of as ecosystem indicators because they possess low ecological resilience due to their low reproductive rate. As habitat quality declines, grizzly bears will be among the first species to display population loss (Eisenberg, 2014; Lamb et al., 2020). Hunting, human settlement, and human-bear encounters all negatively influence bear behavior, and although anthropogenic disturbances have been studied in the past, little information has been released on how we can modify our behavior to avoid damage to bear populations.

In this review, I use brown bear and grizzly bear interchangeably because both subspecies face threats relating to human behavior. Brown bears and grizzly bears belong to the same species, but brown bears typically have access to coastal foods like salmon, while grizzly bears do not (Eisenberg, 2014). It is important to study how human behavior may alter grizzly bear

behavior so that we better understand the implications of "unnatural" bear behavior, or behaviors that bears would not exhibit without human disturbances. Human presence may force grizzly bears to forage in areas with high risks of being hunted or encountering humans, which can lead to decreased fitness and population loss. Understanding the potential consequences of altered grizzly bear behavior is necessary for humans to co-exist with this species while preventing population decline of grizzly bears.

Brown bears are large in size, ranging from 400-1500 pounds with round ears, a round head, and a pronounced shoulder hump. Their pale colored claws are used primarily for digging and catching fish, and have been identified as one of their most intimidating features. The average brown bear diet consists of 10% mammal meat, 5% fish meat, and 80% vegetation, but varies geographically and with resource availability (Eisenberg, 2014). These bears are typically generalists, with an extremely broad diet. Brown bears have one of the lowest reproductive rates of all land mammals, revealing a significant conservation concern. Female grizzlies produce an average of only two young every two to four years, and are very protective of their cubs. Brown bear home ranges are variable but typically range from 50-1000 square miles (Eisenberg, 2014). Bears go through hyperphagia, a period of time when they gain up to several hundred pounds before hibernating. Hyperphagia is extremely important for bears so they are able to maintain nutritional needs during dormancy in the winter (Eisenberg, 2014; Lodberg-Holm et al., 2019). Conservationists have found that grizzly bears thrive where there is an abundance of food, low human presence, and large corridors that connect grizzly populations to one another (Eisenberg, 2014).

When evaluating human-related risks to brown bears, hunting has a strong limiting effect on bear populations, driving habitat selection, foraging strategies, and population dynamics. Hunting grizzly bears is controversial because of its unknown long-term effects on bear density (Mowat et al., 2013). People usually target male bears when hunting because reducing the abundance of male bears increases cub survivorship by diminishing infanticide rates (Miller et al., 2003). In addition, research has suggested that where hunting rates are high, bears are more selective about where they forage and alter their movement patterns to avoid encounters with humans. Shifted movement patterns indicate a problem for bears because the ideal foraging environment may require them to enter habitats with higher risks of being hunted or encountering humans.

It is important to analyze how hunting influences bear populations so that hunting guidelines can be modified based on how brown bear populations respond. Results of capture-recapture studies have confirmed that bears favor areas with no hunting risks, indicating that hunting practices shift bears' foraging patterns (Bischof et al., 2009; Lodberg-Holm et al., 2019; Ordiz et al., 2014; Sakals et al., 2010). For example, researchers were able to uncover patterns of bilberry foraging in response to brown bears' perception of hunting risks. Bears typically consume bilberries before hibernation to gain weight to sustain them through dormancy. Bears selected areas that had a high probability of bilberry occurrence, but differed in this selection where there were higher risks of hunting mortality. Bears chose areas with low bilberry availability because these areas possessed low hunting risks. This reveals that bears will forage in suboptimal conditions to avoid areas with a high risk of being hunted, which over prolonged periods of time, hinders individual fitness (Lodberg-Holm et al., 2019).

Historically, brown bears ranged across most central/western regions of North America, but their past distribution has been reduced because of habitat loss and human persecution (Cristescu et al., 2016). Human settlements expanding into natural areas where bears reside pose risks for brown bear populations. Human development has created gaps in suitable habitats for grizzly populations, minimizing foraging area. Without appropriate connectivity between bear habitats, bears are forced to enter developed areas in order to reach new habitats for foraging (Eisenberg, 2014). Forage quality and quantity are important to brown bears as they prepare to hibernate, and gaps in suitable foraging area may hinder growth during hyperphagia. It is important to consider how bears adjust their behavior to survive in these suboptimal landscapes.

For many animal species, shifts in daily activity patterns may indicate anthropogenicinduced environmental stress. Bears adjust their spatio-temporal use of areas with high human activity, which could be due to stress from human-related activities (Eisenberg, 2014; Lamb et al., 2020). For example, another problematic change in bear behavior in response to human settlement is increased nocturnality, which bears exhibit to ensure survival and reduce conflicts with humans in the area. Although this strategy can be beneficial, there is a trade-off of poor foraging capabilities at night compared to daytime (Lamb et al., 2020). Bears that approach human-dominated areas may able to find sufficient nutrition and reproduce despite reduced visibility white foraging, but the poor survival of the bears in human-dominated areas remains a concern. Ordiz et al. (2014) found that in areas occupied by humans, bear movement was restricted to nocturnal and twilight hours in areas with higher road densities compared to areas without roads. Bears must gain enough fat during hyperphagia to survive the winter, and reduced movement during the daytime makes this more difficult. In this study, bears were more active at night to compensate for less daytime feeding, but the implications of poor visibility while foraging remain unknown (Ordiz et al., 2014). Bears who forage with poor visibility may hinder their individual fitness by spending more time searching for adequate food, and less time feeding.

Brown bears are one of the world's most widely distributed and conflict-prone carnivores, and the frequency of their attacks on humans is increasing. Human perceptions of brown bears and the risks that they pose is also a growing concern. Feeding bears is common in North America, and can cause bears to rely on anthropogenic food sources. Bears obtain human food through supplemental feeding, which includes being fed by humans or eating food that humans leave out and bears take advantage of these extra sources of food. Supplemental feeding motivates bears to approach humans for food, and most research suggests that it can cause bears to rely on these alternative sources of food (Kavčič et al., 2015). Media coverage of human-bear conflicts release misleading information which can cause citizens to overestimate the risk of an attack. When the media covers a story, the main focus is typically information about the attack instead of using the coverage to discuss ways to minimize the risks of human-bear encounters (Bombieri et al., 2019). Video footage of bear attacks gain a lot of public attention, but focus heavily on the people involved and less about the long-term implications of feeding these animals (Moore, 2020). Because bears are dietary generalists, feeding them may incentivize them to approach humans for food, and in turn, increase the risk of human-bear encounters.

To analyze how bears responded to human-bear encounters, researchers approached 33 female and 19 male collared bears in south-central Sweden. None of the bears reacted aggressively to the researchers, and in 84% of the responses, the bears clearly avoided human confrontation. Even though the bears did not display any aggression, they did adjust their daily movement patterns (Ordiz et al., 2013). The bears moved away from humans instead of approaching them, avoiding potential conflict. In Finland, brown bears are fed by tourists and staff, and although this form of tourism is not a typical practice in other countries, bears are fed by humans in other parts of the world as well (Kojola & Heikkinen, 2012). The results of this

study indicated that bears were encountering humans farther away from the feeding sites, contrasting the researchers' hypothesis that the bears would approach humans near these sites. This may indicate that bears are approaching humans outside of the tourism area which displays habituation, or a high tolerance for humans. The researchers recommended the use of GPS and video surveillance to determine if bear behavior is being influenced by human feedings. This study is applicable to North America because humans feed bears in campsites and national parks, which could cause bears to become accustomed to human presence. When bears are less wary of humans, they may be more inclined to approach them with hopes of receiving food, revealing a risk to both bears and humans.

Human-related activities have a profound impact on brown bear behavior and these activities contribute to brown bear population decline all over the world. Understanding how humans influence bear behaviors through hunting, land usage, and human-bear encounters is crucial when creating plans for these species to peacefully coexist. In North America, the effects of human hunting on bear populations should be studied further to potentially modify hunting practices. Mowat et al. (2013) suggest consistently monitoring bear density to calculate allowable kill, and adjusting hunting practices accordingly. Changing hunting regulations may allow bears to forage more freely in risk-free, high-quality habitats (Bischof et al., 2009). Human settlement has forced bears to forage during the night and choose sub-optimal foraging grounds, and some researchers have suggested restricting or limiting human use of roads (Ladle et al., 2018; Ordiz et al., 2014). Other suggestions to mitigate human settlement issues are maintaining movement corridors and ensuring genetic connectivity between bear habitats (Cristescu et al., 2016; Ladle et al., 2018; Ordiz et al., 2014). Implementing these suggestions would allow bears to safely utilize more areas without the trade-off of poor habitat quality or foraging at night. As humans encroach into bear ranges, human-bear encounters are expected to increase, revealing a challenge for North American bear populations (Cristescu et al., 2016). Concrete information on bear behavior should be accessible to people entering bear habitats so that there is a common understanding of how to coexist with bears in these environments. Media coverage on human-bear encounters should place a greater focus on how humans may modify their behavior to ensure natural bear behavior, and include tips for people entering bear habitats. These tips may include carrying pepper spray, making noise, traveling in groups, regulating waste, etc. (Bombieri et al., 2019; Eisenberg, 2014; Sakals et al., 2010). Recognizing how humans influence brown bear behavior and adjusting our behavior accordingly will help facilitate successful coexistence.

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CHAPTER 2. GRANT PROPOSAL

Grizzly Bear Foraging Patterns in Relation to Human Disturbances in Sweden

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November 26, 2020

Section 1: Abstract

Grizzly bear (*Ursus arctos*) populations have faced a troubling history of extirpation, and due to the growing human population, continue to face anthropogenic threats today. Few studies have evaluated how this species responds to anthropogenic disturbances, but this knowledge gap is important to fill to preserve grizzly bear populations in North America where they are currently threatened. Bears prepare for hibernation by entering hyperphagia, a period of time where they forage extensively to maintain metabolic demands for dormancy in the winter. However, anthropogenic threats may limit bear foraging during hyperphagia. I propose to study grizzly bear foraging patterns in Sweden using GPS collar data to assess how bears in hyperphagia forage in response to hunting zones, roads, and human settlement. In addition, my project will investigate what types of human disturbances most influence bear foraging patterns, as well as how time of day influences these patterns. The data collected as part of this study will contribute to conserving grizzly bear populations in North America as an effort to preserve their populations globally.

Section 2: Objectives, Hypotheses, Anticipated Value, Literature Review Objectives

I aim to study grizzly bear foraging patterns in relation to human disturbances (i.e., roads, human settlement, wildlife hunting zones) in south central Sweden. Habitat loss and human persecution have reduced grizzly bears' historic geographic range, and it is important to study what factors influence bear activity patterns so that managers can create protection plans for this species. GPS tracking of grizzly bears will allow us to collect data on bear foraging patterns and investigate how these patterns shift in areas with anthropogenic disturbances. Studying grizzly bear movement in their current range will allow us to evaluate how bear foraging patterns differ

in response to potential anthropogenic risks, which will ultimately help conservationists preserve grizzly bear populations around the world.

Questions and Hypotheses

Q1: How does grizzly bear foraging location in relation to human disturbances (e.g. wildlife hunting, roads, human settlement) vary throughout the day?

H1: Time of day influences the amount of time grizzlies spend in proximity to human disturbances in relation to mortality risks. I expect grizzly bears to forage in areas that are farther away from human disturbances during the day compared to night to avoid human-induced mortality risks.

Q2: Which type of human disturbance most influences where bears forage?

H2: The type of human disturbance will impact the amount of time bears spend foraging due to varying mortality risks to bear populations. Bears will spend less time foraging in hunting zones compared to within 250 m radius of roads and human settlement.

Anticipated Value

Globally, grizzly bears are vulnerable to human-caused mortality, habitat fragmentation due to roads and settlement, and risks of human hunting (Ordiz et al., 2014). Collecting data on grizzly bear foraging patterns in relation to human disturbances in Sweden, where the species is protected, will uncover foraging responses to human hunting, roads, and human settlement. This research will lend insight into what types of human disturbances most impact bear foraging patterns, and will support conservationists as they create management plans for grizzly bears in North America, where grizzlies are listed as a threatened species. Although this study focuses on foraging patterns, GPS collar data can also be used to indicate grizzly bear habitat usage for future research on habitat quality. As humans continue to encroach into grizzly bear habitats, understanding how bears forage in response to human disturbances will contribute greatly to the conservation of grizzly bears.

Literature Review

Grizzly bear populations have had a troubling history of extirpation driven by human hunting practices, and due to the growing human population, they continue to face threats today (Eisenberg, 2014). Grizzly bears are ecosystem indicators because they possess low ecological resilience due to their low reproductive rate. As habitat quality declines, grizzly bears will be among the first species to display population loss (Eisenberg, 2014; Lamb et al., 2020). Additionally, grizzly bears forage extensively to support their generalist diet (Eisenberg, 2014). They go through hyperphagia, a crucial period of time when they gain up to several hundred pounds before hibernating (Eisenberg, 2014). Anthropogenic influences can significantly alter bear foraging behavior (Bischof et al., 2009; Graves et al., 2011; Lodberg-Holm et al., 2019), and it is important to study how bears modify their foraging patterns in response to anthropogenic disturbances.

Conservationists have found that grizzly bears thrive where there is an abundance of food, low human presence, and large corridors that connect grizzly populations to one another (Eisenberg, 2014). Human land usage has created gaps in suitable habitats for grizzly populations, minimizing bear foraging area. Without appropriate connectivity between bear habitats, bears are forced to enter developed areas in order to reach new habitats for foraging, posing a risk for grizzly bear populations (Eisenberg, 2014). As humans encroach on bear habitats, it is important to study how bears modify their foraging behavior in the presence of anthropogenic risks like roads, wildlife hunting zones, and potential for human-bear encounters near settlements.

Some studies have shown how bears respond to anthropogenic threats such as hunting, roads, and human settlement, but there are few studies that investigate all three of these disturbances in relation to grizzly bear foraging patterns. Results of capture-recapture studies have confirmed that bears favor areas with no human hunting risks, indicating that hunting practices shift bears' foraging patterns (Bischof et al., 2009; Lodberg-Holm et al., 2019). Researchers revealed that bears chose to forage in areas with low bilberry availability, despite it being a preferred food resource, because these areas possessed low hunting risks. These results indicate that bears will forage in suboptimal conditions to avoid areas with a high risk of being hunted, which over prolonged periods of time, hinders individual fitness (Lodberg-Holm et al., 2019). In studies that evaluated road density in relation to bear foraging patterns, grizzly bears selected against areas with high road density, foraging in areas near roads far less than in areas away from roads. Many of these studies suggest closing roads to facilitate foraging in habitats near roads (Graves et al., 2011). I predict that bears will forage less in wildlife hunting zones when compared to other human disturbances because human presence as well as loud noises will force bears to forage in other locations.

For many animal species, shifts in daily activity patterns may indicate anthropogenicinduced environmental stress. These changes in activity are important to study to assess how animals respond to their environment and further identify if they are costly to individual fitness. Bears exhibit nocturnality in areas with anthropogenic activity, like human settlement, to ensure survival and reduce conflicts with humans, but there is a trade-off of poor foraging capabilities at night compared to daytime (Lamb et al., 2020). Ordiz et al. (2014) found that in areas occupied by humans, bear movement was restricted to nocturnal and twilight hours in areas with higher road densities compared to areas without roads. Poor visibility while foraging may hinder bears' individual fitness by spending more time searching for adequate food, and less time feeding. I predict that bears will spend more time foraging near human disturbances during the night when compared to during the day to minimize risks to their population.

As humans encroach into bear habitats, it is crucial to study the types of human disturbances that drive bear foraging patterns. Using GPS collars is a common method of tracking movement patterns of large species, and allows researchers to monitor activity patterns in their natural habitats (Ordiz et al., 2014). Data on grizzly bear foraging patterns will allow conservationists to evaluate how bears respond to human disturbances, and can help managers develop plans to minimize the negative effects of these responses. Collecting information on how anthropogenic risks impact grizzly bear populations in Sweden will be critical when taking steps to conserve grizzly bear populations all over the world.

Section 3: Methods

Study Site & Species

To study foraging patterns, I will collect GPS collar data from 102 adult grizzly bears (36 males and 66 females) in Sweden (Ordiz et al., 2014). These bears were fitted for GPS collars for previous studies (e.g., Ordiz et al., 2014), and I will be utilizing these data for my study. There are two main sites that grizzly bears will have access to: Jokkmok in northern Sweden and Hälsingland-Dalarna in central Sweden (Figure 1; Skandinaviska Björnprojektet, 2020). The northern area of Jokkmok includes Sarek National Park, with a subalpine forest and minimal human density of 0.3-1.2 habitants/km². The central area of Hälsingland-Dalarna is filled with coniferous forest, with a human density of 4-7 habitants/km² (Ordiz et al., 2014). The central area possesses several roads due to both logging practices and human settlement (1 \pm 0.5 km/km²). Bears are legally hunted in Sweden with annually established quotas, but are protected in

National Parks and some forests (Ordiz et al., 2013; Ordiz et al., 2014).

Data Collection

Prior to data collection, I will use GIS software to determine the disturbance radius of 250 meters from the outer edges of roads and human settlement (i.e., buildings). Other studies that have evaluated behavioral changes in large animals have used this disturbance radius (Fortin & Andruskiw, 2003). Through GIS software, I will also determine the human hunting disturbance radius, which will be considered within hunting zones. The hunting disturbance radius will not include the disturbance radii for roads and human settlement. Once I map the study sites, I will begin collecting data on grizzly bear foraging patterns. The collars collect GPS positions every 30 minutes, which will be used to determine how much time bears spend within a 250 m radius of roads or human settlement or within hunting zones as well diurnal/nocturnal foraging patterns in relation to these human disturbances. I will consider 5:00AM-9:59PM as diurnal foraging, and 10:00PM-4:59AM as nocturnal forage extensively to meet nutrient requirements for hibernation. I will be using the collar data as a proxy for foraging patterns, as bears that are in hyperphagia forage for 20 hours a day (Nelson et al., 2003).

Data Analysis

To analyze these data, I will carry out Generalized Linear Mixed Models (GLMM) to assess how proximity to human disturbances impacts grizzly foraging time as well as how time of day influences proximity to human disturbances. The response variable for the study will be the number of 30-minute GPS points and their locations, while the predictor variables are the disturbance radii of each type of human disturbance and time of day. To determine if bears foraged closer to human disturbances at night compared to during the day, I will carry out a GLMM with fixed effects of disturbance radii and time of day, with a random effect of sex to account for potential sex differences in foraging patterns. To assess what disturbance impacted bear foraging patterns the most, I will carry out another GLMM with a fixed effect of disturbance radii and a random effect of sex.

Potential Negative Impacts

For this study, the potential for negative impacts are minor, as GPS collars have been used for several decades to track wildlife (Graves et al., 2011; Ordiz et al., 2014). There is potential for constraining the necks of the collared bears if they are on too tight, but professional veterinary staff assisted in putting on the collars (Ordiz et al., 2014). Additionally, bears may alter their behavior in response to the stress from the collars, but this is uncommon (Ordiz et al., 2014). Other than the collars, potential impacts on the environment are not expected.

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Date	Goals	Deliverable
June 9 – June 30, 2021	 Visit study sites Prepare GIS software and identify disturbance radii Train team on collecting information from collars 	- Collect preliminary data on bear foraging patterns (will not contribute to final report)
July 1 – September 30, 2021	- Collect collar data every 30 minutes	- GPS data
October 1 – October 31, 2021	- Data analysis	- Model results
November 1 – November 30, 2021	- Write and submit paper for publication	- Final paper with results

Item	Justification	Cost (unit)	Quantity	Total Cost
Roundtrip Airfare between Denver and Jokkmok, Sweden	For preliminary data collection and to determine disturbance radii at field sites	\$800 round trip	3 (myself + 2 field assistants who will assist in data collection)	\$2400
Lenovo ThinkPad X1 Carbon Gen (16") Laptop + waterproof case	To collect GPS collar data throughout the study period	\$1050	1	\$1050
ArcMap GIS software and R Studio (student)	To map out disturbance radii and create maps for final report	\$100	1	\$100
External Hard Drive	To store a copy of collar data and any additional information needed for the project	\$225	1	\$225
Rental Van for Preliminary Data Collection	To drive between sites and to the housing facility	\$20 per day	21 days	\$420
Gas	To drive between sites and to the housing facility	\$5.50 per gallon	500 miles / 12 miles per gallon = 41 gallons	\$230
Housing Facility	To stay for the duration of preliminary data collection	\$40 per day	21 days x \$40	\$840
Field Assistant Stipend	To assist with data collection and analysis	\$500	\$500 x 2 students	\$1000
Food Budget	Food for 3 weeks in the field	\$30 per day	\$30 x 21 days x 3 people total	\$1890

Section 4: Budget

Total Proposal Request = \$8155

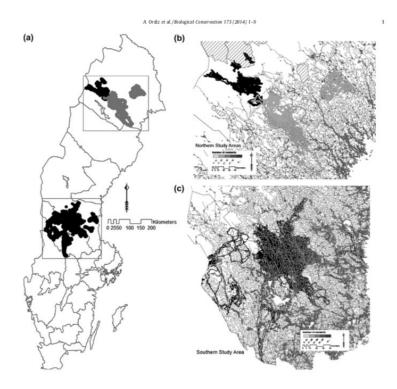


Figure 1. Grizzly bear study area in northern and central Sweden, as defined by the locations of the 102 GPS-radio collared bears from a study conducted by Ordiz et al. (2014). Gray patches are considered northern Sweden and black patches are considered northwest and central Sweden. For this study, we will only be using data from central Sweden. Thin lines represent roads, with highest road density in central Sweden. The gray shading scale represents human population density in the area.



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CHAPTER 3. JOURNAL MANUSCRIPT

Activity Budgets and Social Relationships of Bull Asian Elephants (*Elephas* maximus) at Denver Zoo

Abstract

Limited research has investigated bull elephant behavior and sociality, as bulls are difficult to house and were previously thought to be solitary animals. To assess welfare conditions when in human care, it is important to understand how bulls use their time. Similarly, understanding bull sociality (e.g., affiliative and aggressive behavior; time in proximity) can act as an indicator for welfare. In this study, we assessed the daytime and nighttime activity budget of five bull Asian elephants (*Elephas* maximus) at Denver Zoo and examined how length of social relationships influences nighttime behavior. We hypothesized that due to the diurnal nature of elephants, they would spend their daytime budget exhibiting more active behaviors and less rest. We also hypothesized that at night, new dyads would differ behaviorally from established dyads. From August 2018 – January 2020, we conducted scan sampling of bulls in real-time during the day and while using video footage of bulls at night. During the day, the bulls spent more time exhibiting affiliative and aggressive behaviors, and in proximity to a conspecific, compared to at night. At night, new social dyads and established dyads spent similar amounts of time resting. New social pairings spent more time exhibiting affiliative and aggressive behavior at night, and more time in proximity to their social partner, compared to established dyads. We found that access to additional space increased the odds of bulls resting, both during the day and at night. Managing bull elephants and maintaining compatible social

groupings within the herd can be challenging, but our study suggests that bulls at Denver Zoo possess strong relationships and positive welfare.

Introduction

Determining how zoo animals allocate their time can provide managers with useful insight through the use of behavioral indicators (Horback et al., 2014). Activity budgets demonstrate the frequency of behaviors and can show how animals are responding to current management practices (Horback et al., 2014; Lukacs et al., 2016; Massen et al., 2010). Daytime and nighttime activity budgets are used to evaluate animal well-being by studying the occurrence of natural behaviors and standard proportions of behavioral activity (Horback et al., 2014). Many behavioral studies on Asian elephants (*Elephas maximus*) focus on how they allocate their time during the day, but limited work has assessed their behaviors at night. Behaviors that elephants exhibit during the day may differ significantly at night, when keeper engagement and external stimuli from guests and noise are substantially lower (Posta et al., 2013).

Collecting information on nighttime behaviors of elephants when zoo guests and keepers are not present is a critical step in assessing the welfare of this species under managed care (Holdgate et al., 2016; Lukacs et al., 2016). For example, resting, both standing and recumbent, is essential for the health and welfare of Asian elephants and can be used as a tool to gauge the health of those housed in zoos (Holdgate et al., 2016). Sleep is an important aspect of the circadian rhythm of animals, and abnormal or irregular sleep patterns among elephants can indicate poor health or potential illnesses (Holdgate et al., 2016; Walsh, 2017). Sleeping together in groups or dyads has been demonstrated as a way to identify potential alliances or conflicts within a group (Hartley et al., 2019). In addition, the frequency of feeding behavior and positive social interactions act as additional ways to evaluate how an animal is responding to their environment (Lukacs et al., 2016; Rees, 2009). If elephants exhibit a broad range of natural behaviors and do not show frequent signs of stress (e.g., stereotypy, excessive aggression, etc.), it may be reasonable to conclude that their needs are being met (Rees, 2009). Studies that have assessed both daytime and nighttime elephant behavior have found that elephants spend more time feeding, walking, interacting with enrichment, and resting standing up during the day compared to at night (Holdgate et al., 2016; Horback et al., 2014; Lukacs et al., 2016; Rees, 2009). Previous activity budgets of elephants have also shown that social behaviors, both aggressive and affiliative, occur more often during the day (Horback et al., 2014; Meehan et al., 2016).

Following the departure of staff and guests, a nighttime activity budget of Asian elephants at the San Diego Safari Park showed a spike in positive social behaviors (Horback et al., 2014). Results of the few studies that have investigated nighttime elephant behavior have found that most social behaviors exhibited at night were affiliative, with minimal time spent exhibiting aggressive behaviors (Rees, 2009; Wilson et al., 2006). These studies also suggest that at night, elephants spend a significant amount of time resting, both recumbent and standing up, which is essential for health (Rees, 2009; Koyoma et al., 2012; Wilson et al., 2006). When elephants are under stress at night from daily management changes, they may spend less time resting and more time engaged in stereotypic behaviors (Koyoma et al., 2012). Well-suited social pairings can help decrease the frequency of stress-related behaviors such as stereotypy and abnormal sleep patterns (Lee & Moss, 2014; Massen et al., 2010; Readyhough et al., in review). When possible, activity budgets should aim to include nighttime behavioral data, as elephants should be spending sufficient time resting to support their natural circadian rhythm (Holdgate et al., 2016). Establishing both an in-depth nighttime and daytime activity budgets for Asian elephants is critical for comparing to other Asian elephants both in the wild and in managed care.

Previously thought to be solitary animals, we now know that bull elephants have rich social lives (Evans & Harris, 2014; DeSilva & Wittemyer, 2012). Socialization is important for bull elephants, as they acquire skills and develop relationships that provide benefits to their survival (Evans & Harris, 2008). Social interactions among bull elephants allow them to learn new skills, establish dominance hierarchies, and form social bonds with other elephants (Hartley et al., 2019). Elephant sociality helps optimize animal welfare through stress reduction and opportunities for consistent positive social interactions (Hartley et al., 2019). Adolescent bulls engage in regular social interactions with other bulls, which then persist throughout their lives (Evans & Harris, 2008; Lee et al., 2011). Older bulls facilitate social learning by providing younger bulls with important environmental knowledge and the ability to learn appropriate social and reproductive behaviors (Hartley et al., 2019; Lee & Moss, 2014). Affiliative social behaviors among bulls, such as tactile communication, strengthen social bonds and reduce stress (Massen et al., 2010; Vidya & Sukumar, 2005). Similarly, proximity to a conspecific for long periods of time reflects a certain tolerance for an individual (Massen et al., 2010). Frequent affiliative social behaviors indicate close social bonds with conspecifics and these social associations can improve an individual's reaction to conflicts or stressful events (Massen et al., 2010). Alternatively, bulls exhibit aggressive behaviors such as mounting, charging, and pushing to maintain dominance (Pool, 1987). While some degree of aggression is likely within an established herd as a means to establish and maintain the dominance hierarchy, low levels of aggression among elephants suggests strong social relationships (Ganswindt et al., 2004, Massen et al, 2010).

Compatible social pairings of bulls, however, can be difficult to achieve (Hartley et al., 2019). Bull elephants are difficult to house because they are much bigger and stronger than females, and go through musth, a period of time when they experience elevated hormone levels, heightened sexual interest, and more aggression (Ganswindt et al., 2004; Poole, 1987). Integration of new bulls into an established herd can be challenging for both the elephants and managers, as bulls may need to establish dominance to defend their status or integrate into the dominance hierarchy (Hambrecht & Reichler, 2013). Stress from new integrations can elicit behavioral and physiological reactions in animals, which has been observed through displacement, redirected behavior, and stereotypy (Schmid et al., 2001). Past research has shown that under stress, affiliative behaviors such as play disappear (Lee & Moss, 2014).

Few studies have investigated the effects of bull integration into a previously established herd, but Hambrecht & Reichler (2013) aimed to understand the socialization process of a new male into an existing herd of three bulls at Zoo Hiedelberg. During the weeks directly following introduction, the new male spent less time socializing with other bulls, but after about 4 months, the new bull spent more time exhibiting affiliative behaviors compared to the weeks directly after introduction (Hambrecht & Reichler, 2013). After one year, the bull became increasingly more sociable, spending more time associating with other bulls than alone. Additional evidence of the successful integration into the herd included reduced stereotypical behavior as well as an increase in positive interactions from conspecifics (Hambrecht & Reichler, 2013). In African elephants (*Loxodonta africana*), the frequency of both affiliative and aggressive behaviors in bulls were strongly influenced by the introduction of 2 new female elephants to an established herd of females (Burks et al., 2004). This study showed that over time, both active and passive aggression as well as submissive behavior decreased over the month-long introduction period (Burks et al., 2004). Similar trends were found when introducing new sows to a cattle herd, resulting in a decrease in agonistic interactions over the 3-week study period (Krauss & Hoy, 2011). These studies suggest that the duration of time that animals spend with each other impacts time spent exhibiting both social and non-social behaviors. Understanding elephant sociality can help support management of the species, as bulls engage with their conspecifics to reduce stress through established social bonds. Social relationships positively influence an individual's welfare, therefore it is important to assess the development of social relationships of elephants housed in zoos (Meehan et al., 2016).

Denver Zoo offers the perfect opportunity to compare bull Asian elephants' activity budgets during the day compared to at night to examine how the duration of a social relationship affects nighttime social behavior among dyads. Denver Zoo is home to the largest bachelor herd of bull Asian elephants in North America, comprising 5 male elephants (Readyhough et al., in review; Schreier et al., 2021). In late 2018, two new bulls arrived and began a 5-month quarantine period. Following their quarantine, the new bulls were introduced to the original three elephants, allowing for behavioral comparisons between previously established dyads and new dyads. A previous study on the Denver Zoo elephant herd reported that, when housed with at least one other individual, bulls exhibited fewer stereotypic behaviors compared to when they were alone (Readyhough et al., in review). When housed socially, pacing and head-bobbing decreased when in proximity to another bull (Readyhough et al., in review). This finding indicates that housing bulls together in compatible social groups has the potential to increase welfare through the reduction of stress-induced behaviors. Another study focusing on the introduction of the two new bulls to Denver Zoo's herd found that during the 5-month period following introduction, the odds of engaging in non-contact aggressive behavior were higher

than before the introduction (Schreier et al., 2021). By the end of the study period, all elephants engaged in significantly more affiliative behavior and less non-contact aggressive behavior than during the introduction period, suggesting a stable social dynamic had been established (Schreier et al., 2021). Both of these studies focused on daytime behavior; to date, there have been no studies on the Denver Zoo bull elephant herd's nighttime activity budgets or how nighttime behavior varies between new and established dyads.

In this study, we extend our work on the bull Asian elephant herd at Denver Zoo by including nighttime behavioral data. This study focuses on two main questions: (1) How do bull Asian elephant behaviors (resting, stereotypy, proximity, affiliative and aggressive interactions) differ at night compared to the day? (2) How do nighttime behavior and social interactions differ between established Asian elephant dyads and newer social dyads? We hypothesize that because of the natural circadian rhythm of Asian elephants as well as the lack of external stimuli (guests, noise, etc.) at night, the elephants will dedicate more of their daytime activity budget to active behaviors and more of their nighttime activity budget to resting. Accordingly, we predict that during the day, the elephants will exhibit more affiliative and aggressive behaviors and spend more time in proximity to a conspecific, and less time exhibiting stereotypy and resting compared to at nighttime. Secondly, we hypothesize that at night, new social pairings (i.e., those who were introduced to one another in February 2019) will exhibit different behavioral budgets compared to established social pairings (i.e., relationships that existed before the new bulls were introduced in February 2019) because strong social bonds may not yet be present in these new dyads. We anticipate that elephants in established dyads will exhibit more resting behaviors (both standing and recumbent), affiliative social interactions, and spend more time in proximity

to a conspecific, and less time exhibiting stereotypy and aggressive behaviors when compared with new dyads.

Methods

Study Site & Species

Toyota Elephant Passage (TEP) within Denver Zoo is a multi-yard, rotational exhibit that was built to support the diverse needs of a bachelor elephant herd. The bull Asian elephant herd at Denver Zoo consists of five individuals. Individual 1 (13 y/o), Individual 2 (17 y/o), and Individual 3 (51 y/o) lived together at Denver Zoo and were socialized together regularly for 2.5 years prior to Individual 4 (12 y/o) and Individual 5's (11 y/o) arrival in October 2018. Individuals 4 and 5 are half-brothers who share a father, and were socialized together prior to their arrival at Denver Zoo. After a quarantine period, Individuals 4 and 5 were introduced to the original three bulls through auditory, olfactory, visual, and tactile contact through stall bollards (i.e., "howdy"). Following these initial introductions, physical introductions took place in February 2019, when all elephants were introduced to each other over a week-long period. The addition of Individuals 4 and 5 to Denver Zoo's herd allows for a behavioral comparison between established dyads (combinations of Individual 1, 2, or 3 with Individual 4 or 5).

Data Collection

To address our first hypothesis regarding bull Asian elephant daytime and nighttime behaviors, we conducted instantaneous focal sampling of dyads over 30-minute periods (Altmann, 1974), recording the behavior of each elephant every minute as well as whether the focal animal was in proximity to his conspecific (Table 1). Daytime data were collected by observing the elephants in real time from August 2018 – December 2019 during two daily observation periods: 9:00-11:00 and 13:30-15:30. We collected nighttime data using video footage recorded between 18:00 and 6:00 from February 2019 - January 2020. We aimed to collect similar amounts of data on each elephant and dyad during the day and night, and we rotated focal subjects accordingly. We recorded data using Zoomonitor®, a mobile behavior application developed by Lincoln Park Zoo and Zier Niemann Consulting. Social behaviors were categorized as affiliative (e.g., playing, trunk tangle, body contact) or aggressive (e.g., charge, push, sparring). We defined proximity as within two body lengths of a conspecific (Savage et al., 2008; Soltis, Leong, & Savage, 2015; Bonaparte-Saller & Mench, 2018). To address our second hypothesis and examine how nighttime behavior varied across established vs. new dyads, nighttime behavioral data for new social pairings were compared to those for established pairings. We coded nighttime videos such that we have similar amounts of data for new dyads and established dyads.

Data Analyses

We based our analysis of daytime and nighttime activity budgets of bull Asian elephants on a total of 731.5 hours of focal observations (1,463 30-minute samples) when elephants were housed with one other bull. Of these observations, 181 hours (362 30-minute samples) were from daytime sampling, while 550.5 hours (1,101 30-minute samples) were from nighttime sampling. To address our second hypothesis regarding nighttime behavior across new and established dyads, previously established social dyads account for 256 hours (480 30-minute samples), while new social dyads make up 294.5 hours (587 30-minute samples) of the nighttime dataset. Our analyses include only data on dyads of bull Asian elephants and do not include data on elephants when housed alone or with more than two bulls as thus far our nighttime dataset consists only of dyads. Behavioral data were first converted into binary values (behavior category occurred = 1, another behavior occurred = 0) for each sample using the *dplyr* package in *R* (version 3.4.1., R Core Team, 2017). Following this step, we calculated the proportion of scans for each 30-minute sample during which each behavior was performed.

To test our first hypothesis, we used generalized linear models (GLM) with a binomial distribution to calculate the odds of engaging in a specific behavior during the daytime compared to at night. Similarly, to address our second hypothesis, we used GLM to calculate the odds of behaviors occurring in new dyads compared to established dyads. GLMs are appropriate for these analyses as the data represent binomially-distributed proportions that violate assumptions of simple linear regressions. The fixed effects used in our models remained consistent across both hypotheses, and included which other bulls were in musth, access area, inside/outside access, and focal animal, as well as an interaction term between access area and inside/outside access. When analyzing the daytime and nighttime data to test our first hypothesis, we used an additional fixed effect indicating when the session occurred (during the day or night). We chose models with the lowest Akaike Information Criterion (AIC) as our best model for each behavior (Tables 1 - 6). We used open source statistical software *R* to conduct all analyses; values p<0.05 were considered statistically significant.

Resting			
Daytime vs. Nighttime			
Model	AIC	Deviance	
RestingProp ~ DayNight + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	1165	644.72	
RestingProp ~ DayNight + InOutAccess + AccessArea + Musth + FocalName	1165.7	648.4	
RestingProp ~ DayNight + InOutAccess + Musth + FocalName	1179.9	660.47	
RestingProp ~ DayNight + InOutAccess + FocalName	1187	671.93	
RestingProp ~ DayNight + FocalName	1197.4	690.96	
RestingProp ~ DayNight	1249	741.59	
New Dyads vs. Established Dya	ds		
Model	AIC	Deviance	
RestingProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	1191.9	632.94	
RestingProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	1191.4	636.29	
RestingProp ~ NewSocial + InOutAccess + Musth + FocalName	1413.5	751.79	
RestingProp ~ NewSocial + InOutAccess + FocalName	1423.3	760.63	
RestingProp ~ NewSocial + FocalName	1469.8	808.97	
RestingProp ~ NewSocial	1510.5	850.33	

Table 1. Model selection table for GLM of resting behavior (bold indicates final model).

Table 2. Model selection table for GLM of standing and recumbent resting behavior at night (bold indicates final model).

Nighttime Resting		
Standing Up		
Model	AIC	Deviance
StandingUpProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	802.4	391.46
StandingUpProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	803.2	395.38
StandingUpProp ~ NewSocial + InOutAccess + Musth + FocalName	956.8	483.48
StandingUpProp ~ NewSocial + InOutAccess + FocalName	957.5	487.31
StandingUpProp ~ NewSocial + FocalName	979.2	501.77
StandingUpProp ~ NewSocial	991.7	526.85
Lying Down		
Model	AIC	Deviance
LyingDownProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	953.8	760.59
LyingDownProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	950.1	760.82
LyingDownProp ~ NewSocial + InOutAccess + Musth + FocalName	1119.4	902.77
LyingDownProp ~ NewSocial + InOutAccess + FocalName	1136.3	923.24
LyingDownProp ~ NewSocial + FocalName	1161	950.47
LyingDownProp ~ NewSocial	1198.4	998.24

Affiliative Behavior Daytime vs. Nighttime		
AffiliativeProp ~ DayNight + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	223	119.75
AffiliativeProp ~ DayNight + InOutAccess + AccessArea + Musth + FocalName	218.6	121.64
AffiliativeProp ~ DayNight + InOutAccess + Musth + FocalName	216.5	121.68
AffiliativeProp ~ DayNight + InOutAccess + FocalName	210	126.14
AffiliativeProp ~ DayNight + FocalName	206.1	127.75
AffiliativeProp ~ DayNight	194.2	134.51
New Dyads vs. Established Dya	ds	
Model	AIC	Deviance
AffiliativeProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	96.9	85.39
AffiliativeProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	92.8	87.67
AffiliativeProp ~ NewSocial + InOutAccess + Musth + FocalName	100.3	102.80
AffiliativeProp ~ NewSocial + InOutAccess + FocalName	98.3	103.18
AffiliativeProp ~ NewSocial + FocalName	86.1	109.81
AffiliativeProp ~ NewSocial	84.4	114.91

Table 3. Model selection table for GLM of affiliative behavior (bold indicates final model).

Aggressive Behavior		
Daytime vs. Nighttime		
Model	AIC	Deviance
AggressiveProp ~ DayNight + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	162.8	112.44
AggressiveProp ~ DayNight + InOutAccess + AccessArea + Musth + FocalName	159.4	113.72
AggressiveProp ~ DayNight + InOutAccess + Musth + FocalName	157.5	119.56
AggressiveProp ~ DayNight + InOutAccess + FocalName	155.6	119.56
AggressiveProp ~ DayNight + FocalName	144.4	132.23
AggressiveProp ~ DayNight	140.4	132.87
New Dyads vs. Established D	yads	I
Model	AIC	Deviance
AggressiveProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	63.5	52.71
AggressiveProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	59.5	52.79
AggressiveProp ~ NewSocial + InOutAccess + Musth + FocalName	61.5	61.23
AggressiveProp ~ NewSocial + InOutAccess + FocalName	59.7	61.95
AggressiveProp ~ NewSocial + FocalName	46.6	70.08
AggressiveProp ~ NewSocial	43.4	114.91

Table 4. Model selection table for GLM of aggressive behavior (bold indicates final model).

Stereotypic Behavior		
Daytime vs. Nighttime		
Model	AIC	Deviance
StereoProp ~ DayNight + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	38.2	9.65
StereoProp ~ DayNight + InOutAccess + AccessArea + Musth + FocalName	34.2	9.65
StereoProp ~ DayNight + InOutAccess + Musth + FocalName	28.2	10.54
StereoProp ~ DayNight + InOutAccess + FocalName	26.2	10.65
StereoProp ~ DayNight + FocalName	14.2	13.29
StereoProp ~ DayNight	10.2	13.79
New Dyads vs. Established Dya	ıds	L
Model	AIC	Deviance
StereoProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	31.9	3.11
StereoProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	27.9	3.17
StereoProp ~ NewSocial + InOutAccess + Musth + FocalName	26.2	4.79
StereoProp ~ NewSocial + InOutAccess + FocalName	24.2	4.80
StereoProp ~ NewSocial + FocalName	12.2	7.41
StereoProp ~ NewSocial	8.2	7.63

Table 5. Model selection table for GLM of stereotypic behavior (bold indicates final model).

Proximity			
Daytime vs. Nighttime			
Model	AIC	Deviance	
NearProp ~ DayNight + InOutAccess + AccessArea + Musth +	1635.7	711.96	
(InOutAccess * AccessArea) + FocalName			
NearProp ~ DayNight + InOutAccess + AccessArea + Musth + FocalName	1635.4	712.88	
NearProp ~ DayNight + InOutAccess + Musth + FocalName	1645.1	721.82	
NearProp ~ DayNight + InOutAccess + FocalName	1645.7	722.35	
NearProp ~ DayNight + FocalName	1651.7	739.70	
NearProp ~ DayNight	1658.7	754.11	
New Dyads vs. Established Dya	ads		
Model	AIC	Deviance	
NearProp ~ NewSocial + InOutAccess + AccessArea + Musth + (InOutAccess * AccessArea) + FocalName	1185.2	626.62	
NearProp ~ NewSocial + InOutAccess + AccessArea + Musth + FocalName	1183	627.11	
NearProp ~ NewSocial + InOutAccess + Musth + FocalName	1286.3	736.11	
NearProp ~ NewSocial + InOutAccess + FocalName	1284.8	736.14	
NearProp ~ NewSocial + FocalName	1307.9	764.30	
NearProp ~ NewSocial	1321.6	777.77	

Table 6. Model selection table for GLM of proximity (bold indicates final model).

Results

Daytime vs. Nighttime Activity Budgets

As expected given the diurnality of elephants, the bulls spent a significantly lower percentage of scans resting during the day (2.3%; 95% CI: -44.8% - 49.4%) compared to at night (47.1%; 95% CI: -30% - 124%). This translates to a 48.5% increase in the odds of resting at night (95% CI: 16.2% - 142%; p<0.05; Figure 1). The percentage of affiliative behaviors was lower at night compared to the day: the bulls spent 13.4% of scans exhibiting affiliative social behaviors during the day (95% CI: -9.1% - 35.9%) compared to 3.8% of scans at night (95% CI:

-10.8% - 18.4%). This difference represents a significant 75.2% decrease in the odds of exhibiting affiliative behaviors at night (95% CI: 60.8% - 84.4%; p<0.05; Figure 1). As expected, the frequency of aggressive behaviors also significantly decreased at night. The elephants spent 7.8% of scans exhibiting aggressive behaviors during the day (95% CI: -17.5% -33.2%) compared to 1.5% of scans at night (95% CI: -8.8% - 11.7%), translating to a significant 85.7% decrease in the odds of exhibiting aggressive behaviors at night (95% CI: 72.3% - 92.7%; p<0.05; Figure 1). Overall, the elephants engaged in very little stereotypic behavior. During the day, the elephants spent 0.6% of scans exhibiting stereotypy (95% CI: -0.54% - 1.7%), while at night they spent only 0.2% of scans engaged in stereotypy (95% CI: -2.8% - 3.2%), representing a 50% decrease in the odds of stereotypic behaviors occurring at night, although this difference was not significantly different than 0 (95% CI: -8.36% - 97%; p=0.72; Figure 1). The bulls spent 56.2% of scans in proximity to a conspecific during the day (95% CI: 5.5% - 107%) compared to 40.8% of scans at night (95% CI: -31.9% - 113%), which represents a significant 61.6% decrease in odds of spending time in proximity to a conspecific at night (95% CI: 43% - 74.2%; p<0.05; Figure 1).

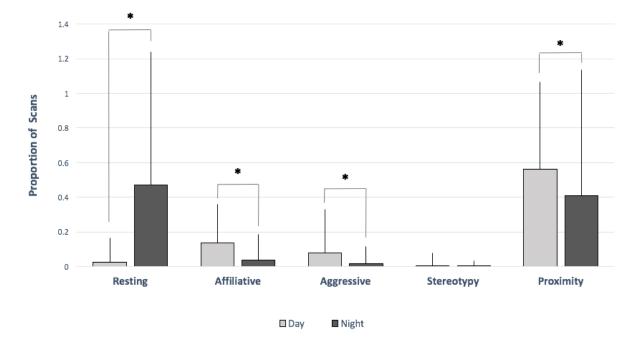


Figure 1. Behavioral activity budgets of bull elephants differ significantly between the day and night. Light gray bars indicate daytime observations and dark gray bars indicate nighttime observations. Error bars show the 95% confidence intervals of the proportion of scans that bulls spent exhibiting each activity.

* indicates p<0.05

Differences in New vs. Established Social Pairings

Contrary to expectations, there were no significant differences in overall time spent resting among new dyads (46.9%; 95% CI: -29.4% - 123%) compared to established dyads (46.2%; 95% CI: -28.9% - 121%). This pattern held when examining standing rest and recumbent rest separately. There was no difference in standing rest between new (23%; 95% CI: -33.7% - 79.7%) and established social pairings (21.6%; 95% CI: -31.2% - 74.5%), nor in recumbent rest (new dyads: 23.7%; 95% CI: -53.6% - 100%; established dyads 24%; 95% CI: -50.5% - 98.5%; Figure 2). Bulls in new dyads engaged in greater proportions of social behavior than established dyads. Bulls in new social pairings spent 3.9% of scans exhibiting affiliative behavior (95% CI: -11.3% - 19.1%) and established social pairings spent 3.2% of scans exhibiting these behaviors (95% CI: -9.6% - 16.1%), representing a 21.3% increase in the odds of exhibiting affiliative behavior in new social dyads (95% CI: -36% - 131%; p=0.56; Figure 2). Similarly, new dyads spent 1.8% of scans exhibiting aggressive behavior (95% CI: -9.6% -13.1%), while established dyads spent 0.9% of scans exhibiting aggression (95% CI: -6.4% -8.2%), translating to a 101% (95% CI: -33.8% - 512%; p=0.22; Figure 2) increase in the odds of exhibiting aggression as a new social pairing. The change in odds were not statistically significant for either social behavior category. Bulls in both new and established social dyads engaged in very little stereotypic behavior. New social dyads spent 0.27% of scans engaging in stereotypy, while established dyads were not observed exhibiting stereotypy during the study period. Contrary to predictions, the bulls in new dyads spent 41.2% of scans in proximity to a conspecific (95% CI: -32.1% - 115%), while established dyads only spent 26.7% of scans in proximity to another bull (95% CI: -40% - 93.4%), representing a significant 39.6% increase in the odds (95% CI: 0.8% - 93.3%; p<0.05; Figure 2).

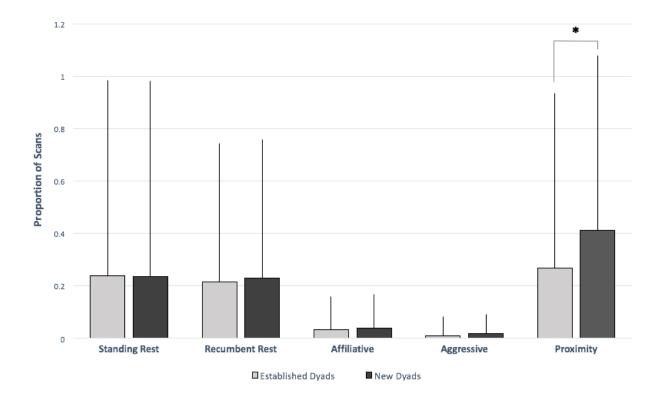


Figure 2. Proportion of scans that bulls spent in proximity to their social partner, but no other behaviors differed between new and established social dyads. Light gray bars indicate established social pairings and dark gray bars indicate new social pairings. Error bars show the 95% confidence intervals of proportion of scans that dyads spent exhibiting each behavior. * indicates p<0.05

Other Significant Factors

Additional co-predictors in the models had significant effects on bull behavior. Across both daytime and nighttime data, when bulls had access to both indoor and outdoor areas, the odds of resting significantly increased compared to when the bulls had access to either only indoor or only outdoor facilities (p=0.028). Additionally, an increase in access area significantly decreased the odds of the elephants resting (p<0.05). When the elephants had only access to outdoor facilities, the odds of spending time in proximity to a conspecific significantly decreased compared to when the bulls had access to both indoor and outdoor areas (p<0.05). At night, when bulls had access to only outdoor facilities, the odds of them being in proximity to their social partner at night increased (p=0.029).

Bulls were typically housed alone when in musth; however, a musth bull's presence may affect the behavior of bulls in nearby areas. Across both daytime and nighttime data, there was a 110% increase in the odds of resting when Individual 2 was in musth (95% CI: 36.8% - 221%; p<0.05). Based on just the nighttime observations, when Individual 2 was in musth, the odds of other bulls spending time in proximity to their conspecific overnight increased by 125% (95% CI: 44.4% - 249%; p<0.05).

Discussion

Summary of Findings

The behavior of bull Asian elephants at Denver Zoo significantly differed across daytime and nighttime. As predicted, bulls spent less time resting and more time exhibiting affiliative and aggressive behaviors, and in proximity to a conspecific, during the day compared to night. Additionally, time since introduction played a role in nighttime behavior between new and established social dyads. Contrary to predictions, new social pairings spent significantly more time near their conspecific compared to established dyads. While differences in social behavior were not statistically significant, there was a trend of new social dyads engaging in more social behavior – both affiliative and aggressive – than established dyads. Our results revealed no differences in resting among new and established social pairings.

Resting

Resting is essential for the health and welfare of animals (Evison et al., 2020; Schiffmann et al., 2018), yet few studies have focused on the resting behaviors of animals in human care (Holdgate et al., 2016). The quality and quantity of sleep can have physiological, behavioral, and

psychological consequences on animals (Brando & Buchanan-Smith, 2018; Schiffmann et al., 2018). Sleep deprivation can disrupt vital biological processes; therefore, it is important for managers to ensure that their animals get enough rest (Holdgate et al., 2016; Schiffmann et al., 2018). Elephants are diurnal, spending most of their day feeding, staying active, and walking, and most of the night resting (Walsh, 2017). The results from our daytime and nighttime observations at Denver Zoo align with previous findings showing that elephants spend more time resting at night than during the day (Holdgate et al., 2016; Horback et al., 2014; Lukacs et al., 2016; Rees, 2009). Under proper welfare conditions, elephants should spend a minimum of 15-30% of their time resting (Evison et al., 2020; Horback et al., 2014). Bulls in our study spent about half (47.1%) of nighttime observations resting, suggesting appropriate welfare at Denver Zoo (Evison et al., 2020).

At night, there was no difference between new and established social pairings in the proportion of scans spent resting. This trend held true when examining standing and recumbent rest separately. Recumbent rest, or rest while lying down, is the optimal opportunity for elephants to enter REM sleep, and thus, acts as an indicator of their welfare (Schiffmann et al., 2018). Social factors can also affect sleep and resting in animals, where well-suited social groups support sufficient rest, and social stress reduces the frequency of resting behaviors (Brando & Buchanan-Smith, 2018; Meehan et al., 2016). Both new and established dyads spent similar proportions of scans resting at night and exceed the welfare recommendation for rest, suggesting little social stress among the bulls at Denver Zoo.

Affiliative and Aggressive Behaviors

The frequency of affiliative and aggressive social behaviors in Asian elephants can also be used to evaluate their welfare, as the absence of positive social behaviors or increase in aggressive behaviors may indicate stress (Lee & Moss, 2014). Affiliative social behaviors can act as an indicator for integration and stress levels, as play is not essential for survival and is regarded as low priority (Hambrect & Reichler, 2013). Bulls in our study exhibited significantly more affiliative and aggressive behavior during the day compared to at night. Similarly, Horback et al. (2014) showed that the frequency of positive and negative social behaviors among 15 African elephants in an outdoor zoo was higher in daylight hours compared to nighttime. In wild herds, elephants also spend a significant proportion of the day maintaining relationships with other individuals through frequent interactions with conspecifics (Horback et al., 2014; Lee & Moss, 2014).

Following the integration of Individuals 4 and 5 into the herd, we expected new social dyads to exhibit more aggressive behavior and less affiliative behavior compared to established dyads when housed together overnight. During nighttime, bull elephants at Denver Zoo exhibited more affiliative behavior than aggressive behavior regardless of their social partner, indicating strong social relationships among all individuals (Bonaparte-Saller & Mench, 2018; Ganswindt et al., 2004, Massen et al, 2010). While differences were not statistically significant, new social pairings exhibited both more affiliative and aggressive behaviors at night compared to established pairs. During the introduction of Individual 4 and 5 to the existing herd at Denver Zoo, the bulls also showed an increase in affiliative and aggressive behaviors during the day (Schreier et al., 2021). After the five-month introduction, then bulls exhibited more affiliative behaviors and less aggression, acting as evidence towards successful integration (Schreier et al., 2021). Hambrecht & Reichler's (2013) study at Heidelberg Zoo aimed to integrate a single bull into an existing herd of three bulls. In the months directly following introduction, the new bull engaged in more aggression and less affiliative interactions compared to the other bulls

(Hambrect & Reichler, 2013). After a year of integration, the new bull became more sociable, less aggressive, and spent more time in proximity to conspecifics compared to earlier in the introduction (Hambrect & Reichler, 2013). The increase in affiliative interactions and decrease in aggression found in Hambrect & Reichler's (2013) study align with what we found among new dyads at Denver Zoo.

Elevated levels of aggression may suggest poor welfare or social stress (Massen et al., 2010; Szott et al., 2019), but bulls at Denver Zoo exhibited low aggression across the entire sampling period. While all dyads in our study spent little time exhibiting aggression at night, it was twice as high among new dyads. In these pairings, the bulls may have employed increased aggression to defend and establish their position in the dominance hierarchy (Seltmann et al., 2019). Bulls in established dyads most likely have a better understanding of where they stand in the dominance hierarchy, and do not need to exert aggression to make this determination (Doughty et al., 2014).

Proximity

Measures of friendship in primate research have used proximity and affiliative body contact to determine social associations (Massen et al., 2010), and this may be the case for other social animals as well, including elephants. Close proximity to another individual is unlikely to arise by chance, and often represents a certain tolerance for a conspecific (Bonaparte-Saller & Mench, 2018; Massen et al., 2010). The bulls in our study spent a greater percentage of scans in proximity to a conspecific during the day than at night. Interestingly, contrary to our prediction, new social pairings spent a greater proportion of nighttime scans in proximity to their conspecific compared to established social dyads. Male elephants often spend time associating with other males to determine each other's status or dominance, and the bulls at Denver Zoo spent more time near new social partners (Seltmann et al., 2019). This suggests that while social bonds are strong among the herd overall, new social dyads are investing more time into these recently formed relationships in order to establish a dominance hierarchy (Massen et al., 2010; Seltmann et al., 2019). Under stress caused by unfamiliar habitats, African elephants did not invest time into forming relationships with new conspecifics (Pinter-Wollman et al., 2009), suggesting that the bulls at Denver Zoo are under minimal stress and are able to strengthen these newly-formed relationships. Ensuring group compatibility among bull elephants can be extremely challenging, but our findings show that bulls at Denver Zoo exhibited more affiliative than aggressive behaviors and new social pairings spent more time in proximity to their conspecific to develop these relationships.

Stereotypy

Elephants can exhibit a variety of stereotypic behaviors as a reaction to sudden changes in management, social stress, or lack of positive stimuli (Koyoma et al., 2012). Following daily management changes, an African elephant at the Higashiyama Zoo in Japan exhibited a spike in stereotypic behaviors during the day that declined over time (Koyama et al., 2012). In a herd of wild African elephants, stress from game drive vehicles increased stereotypic behaviors, highlighting how stress can influence behavior (Szott et al., 2019). The introduction of new individuals into a herd may cause behavioral stress that is often observed through increased stereotypy and elevated levels of aggression (Horback et al., 2014; Schmid et al., 2001), but as new elephants successfully integrate, these behaviors should decrease (Hambrecht & Reichler, 2013). Established pairings at Denver Zoo exhibited no stereotypy, which suggests no social stress between these dyads. New social pairings spent less than 0.5% of scans exhibiting stereotypy, and all of these were carried out by Individual 3 when housed with Individual 5. Based on keeper observations and unpublished data, Individual 3 exhibits the most stereotypy in the herd, both when alone and when housed with conspecifics, potentially due to his geriatric age (51 y/o). Oxidative stress increases with age in humans (Mendoza-Núñez et al., 2007), which may also be the case for elephants. The results of our study at Denver Zoo - showing minimal stereotypy within the herd among both new and established dyads - indicate little stress among the bulls.

Other Significant Factors

In our study, we found that access to both indoor and outdoor facilities, and access to larger areas, significantly increased the odds of bulls resting. Similarly, a zoo African elephant who experienced an additional acre of outdoor space at night increased recumbent rest by about a half hour each night (Holdgate et al., 2016). Providing elephants with more space and opportunities to access indoor and outdoor facilities can reduce stress (Greco et al., 2017). Stress from physical environments has the potential to negatively impact rest (Evison et al., 2020; Greco et al., 2017), and offering elephants increased opportunities to interact with more of their surroundings will improve welfare (Greco et al., 2017; Holdgate et al; 2016).

The results of our study revealed that when Individual 2 was in musth (and housed alone), the other bulls spent more time resting and in proximity to a conspecific. Male elephants go through musth, a period of sexual activity where they experience elevated testosterone levels (Evans & Harris, 2008). Musth bulls are typically more aggressive, exhibiting more dominant and moody behavior (Seltmann et al., 2019). Heightened aggression during this period is one of the main reasons bulls are housed alone when in musth. Individual 2 is the second most dominant bull in the group, while Individual 3, who is geriatric, is the most dominant. When in musth and due to his dominance status within the herd, Individual 2 may act as a bigger threat to

the younger bulls (Doughty et al., 2014). When housed away from the rest of the herd, the other bulls are able to spend more time resting and with their conspecifics, as the stress from a dominant bull in musth is eliminated.

Implications for Animal Welfare

Decision-making regarding animal welfare should use an evidence-based approach to ensure high quality of care (Brando & Buchanan-Smith, 2018). Behavioral observations provide many advantages for animal care staff, allowing behaviors to be quantified and evaluated to determine the welfare of an individual or group of animals. Managers are responsible for their animals' access to space and opportunities for social companionship, which are crucial to animal welfare (Brando & Buchanan-Smith, 2018). Based on our observations, bull Asian elephants at Denver Zoo obtain sufficient rest, exhibit positive social behaviors, and minimal stereotypy. Following the addition of Individuals 4 and 5 to the herd, the bulls demonstrated frequent affiliative behaviors and time spent in proximity to new social partners at night. New social dyads spent more time in proximity to their social partners and exhibited more aggression compared to established dyads, which suggests they are still assessing each other's dominance and strengthening these new relationships. Low levels of aggression and little stereotypy within the herd demonstrate successful integration and positive social relationships among all individuals. Keepers and managers should aim to provide appropriate social groupings for their animals, as social bonds are known to buffer stress, reduce stereotypy, and improve welfare (Brando & Buchanan-Smith, 2018). Our study also revealed the effect of exhibit access and size on resting behaviors of bull elephants, and we recommend that, when possible, managers provide elephants with access to both indoor and outdoor facilities with as much space as possible to

reduce stress and promote rest. Future behavioral research on the activity budgets of bull elephants and their sociality can help support the welfare of Asian elephants in managed care.

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CHAPTER 4: STAKEHOLDER ANALYSIS

Loris Trade is not so Slow: Conservation and Welfare of Slow Lorises

Introduction

In 2013, a video of a slow loris being fed a rice ball reached over 13 million views on YouTube. This video received a lot of attention from the public, with a comment section filled with people discussing how cute the loris was. While the video received positive attention, it also highlighted major concerns for slow loris welfare, as bright lights, small cages, and improper diets all contribute to their low survival rate in captivity (Nekaris et al., 2016). Although owning a slow loris remains illegal worldwide, several hundred videos of captive lorises posted on social media platforms continue to fuel the demand for exotic pets. Thousands of lorises are traded annually, and due to the lack of enforcement, their populations are becoming increasingly rare (TRAFFIC, 2010).

All five species of slow lorises have been listed as either critically endangered (Javan slow loris (*Nycticebus javanicus*); Figure 1)) or vulnerable (Bengal slow loris (*Nycticebus bengalensis*), Bornean slow loris (*Nycticebus borneanus*), Sunda slow loris (*Nycticebus coucang*), and pygmy slow loris (*Nycticebus pygmaeus*) on the International Union for Conservation of Nature (IUCN) red list for the last decade (Nekaris et al., 2020), and the thriving trade for wildlife acts as a major contributor to their rapid population decline. Although the slow loris trade remains illegal globally, prosecuting sellers and owners can be extremely challenging. Slow lorises are protected under both the Endangered Species Act and Lacey Act in the United States, but the capturing and selling of lorises begins in the forests where they reside. Many of these forests are in Indonesia, where laws governing the illegal wildlife trade are not strictly

enforced (IAR, 2021). While law enforcement authorities can work to stop the trade before lorises are sold, investigations on capturers and sellers can be time consuming and difficult, as a large portion of the trade occurs online (IAR, 2021). Trades occurring on online platforms make law enforcement challenging due to fleeting listings, encrypted messaging, and offline conversations (Coalition Report, 2020). Once removed from forests, slow lorises are difficult to house successfully, as they are nocturnal primates with venomous bites. For this reason, their teeth are often removed in human care, compromising their natural diet (Nekaris & Starr, 2015). This act makes it challenging for lorises to survive when released back into the wild, further contributing to the loss of slow loris populations in the wild.

I propose the development of animal care criteria derived from collaborative efforts between law enforcement officials in the United States and animal experts from the International Animal Rescue (IAR) in an effort to provide welfare guidelines for slow loris owners. Decriminalizing the ownership of lorises within the United States will also act as a short-term solution, so that owners of lorises must act in accordance with the Animal Welfare Act to ensure healthy animals. Strict criteria for loris owners will also promote the return of lorises to humane rescue agencies or the wild, as slow loris welfare is challenging to achieve. If loris owners are unable to act in accordance with the criteria, the lorises will be surrendered to rescue agencies. While the short-term solution is in action, law enforcement officials should work with slow loris rescue agencies and former traders to stop the trade before animals are in human care. Long-term collaboration between U.S. law enforcement and IAR researchers will support the stabilization and recovery of slow loris populations in the wild. The illegal trade for slow lorises is the biggest threat to the survival of the species, and without successful intervention, slow lorises will remain in danger of extinction.



Figure 1. Javan slow loris (Nycticebus javanicus), listed as Critically Endangered on the ICUN Red List.

Slow Loris Behavioral Ecology, Trade, and Demand

Behavioral Ecology

Slow lorises have received a lot of attention for looking similar to teddy-bears, with large, forward facing eyes (Lombardi, 2016). The size of these primates is also desirable for those who want to own an exotic animal but have limited space, as they only reach about 3-4 pounds (Figure 1). The behavior of slow lorises is poorly understood, as these animals reside in the upper canopy of the forest and are therefore difficult to study (Fam et al., 2014; Nekaris & Starr, 2015). Their slow birth rate is another reason their populations are threatened in the wild, as females only bear a maximum of one offspring every one and a half years (ProFauna Indonesia, 2007). As nocturnal primates, they are most active at night, making studies on their populations difficult. Slow lorises are gouging specialists, using their lower front teeth to anchor their teeth into food items such as arthropods, flowers, fruit, and nectar (Nekaris & Starr, 2015). Lorises use their lower anterior teeth to pierce the cambium of trees in the wild to consume sap, a large

component of their diet in the wild (Wiens, 2002). Additionally, slow lorises are the only venomous primates, using oil from the brachial gland in their mouth to inject venom into their victims (usually other lorises) or lick their fur to avoid ectoparasites (Nekaris et al., 2013). When in human care, their teeth are often removed to protect the owner from the properties of the venom (Figure 2). Loris venom triggers autoimmune responses and bacterial pathogenesis in humans, usually leading to severe rashes that worsen over time without intervention (Nekaris et al., 2013). Once their teeth are removed, lorises are unable to be released, as they cannot feed naturally in the wild (IAR, 2021; Nekaris et al., 2013). Despite risks from their venom, the combination of social media posts and the small, cute appearance of lorises makes them a prime target for the illegal pet trade.

Slow Loris Trade

It has been estimated that about 30-90% of slow lorises do not survive the stress from being taken from the wild (Hance, 2012). For every one loris sold, it is estimated that four lorises die during transport to their destination (Gaworecki, 2017). Mortality rates of captured lorises are high due to transport conditions which include cramped, poorly ventilated crates that cause wounds, stress, and other serious medical problems (Gaworecki, 2017). Slow lorises are traded openly in bird markets and even some pet shops in Indonesia (IAR, 2021; Nijman & Nekaris, 2014). Slow lorises in Indonesian markets are sold for approximately \$70 USD, and are widely available (Nijman et al., 2017). The demand and ongoing trade of slow lorises in Indonesia impedes conservation goals, and because of the poor enforcement from the Indonesian government, sellers are not deterred from carrying out the trade internationally (Nijman et al., 2017). The demand for exotic pets is highest in the United States, and once wildlife crosses US borders, it is often difficult to monitor the scope of the trade (Department of Justice, 2021). Little

is known about how many lorises are owned as pets within the US; however, thousands of lorises are taken from forests each year for the trade (ProFauna Indonesia, 2007).

Slow loris trade and ownership has been investigated to assess how lorises fare in captivity. Nekaris et al. (2016) focused on 5 core factors to measure the welfare of animals: freedom (1) from hunger, thirst, and malnutrition, (2) from disease and injury, (3) from physical forms of discomfort due to thermal, resting, or other environmental conditions, (4) from fear, distress, and negative psychological states, and (5) to carry out natural/normal behaviors. The authors suggest that failing to provide these freedoms raises ethical concerns and highlights the unsuitability of an animal as a pet (Nekaris et al., 2016). When investigating animal welfare, the authors found that within their sample size of 100 popular social media videos of slow lorises, each video showed at least one freedom violated. One-third of the videos showed all 5 freedoms violated, suggesting that uninformed individuals are unable to provide a good standard of welfare for slow lorises. It is difficult to keep a slow loris as a pet while accomplishing all 5 freedoms because this would require replicating natural conditions and regularly monitoring loris behavior.

Demand for Slow Lorises as Pets

Social media has played a significant role in the demand for slow lorises and other exotic animals. Images of exotic pets across social media platforms can increase the demand for these unique animals, fueling the trade of exotic species (Nekaris et al., 2016). Over the last decade, slow lorises have become a popular phenomenon in videos online, gaining positive acceptance by viewers. Hundreds of videos on different social media platforms depict lorises feeding, playing, and sleeping, and the videos' popularity directly contributes to the desire to own unique pets (Nekaris et al., 2016). Several of these videos have shown owners tickling slow lorises, which recent studies have shown can actually be harmful to them (Nekaris et al., 2016). In addition, celebrities like Lady Gaga and Rihanna have taken videos and photos with slow lorises without commenting on the implications of illegal wildlife trade.

Stakeholders

International Animal Rescue

The International Animal Rescue (IAR) located in Java, Indonesia is the only animal rescue at present that rehabilitates slow lorises. The IAR works to stop the trade of slow lorises and other species, while rehabilitating and releasing those that have been rescued from the trade back into the wild. As of 2021, the IAR has rescued over 1000 slow lorises and rehabilitated about 670 back into the wild (IAR, 2021). About 30% of rescued lorises have had their teeth removed, and because this prevents natural feeding, they are housed at the IAR (Figure 2). The IAR is considered an educational facility in Java, where guests can visit and learn more about threats to slow loris populations. Rehabilitation and release is challenging for animals that have been living under human care because of habituation, or the familiarity of living/feeding conditions that are different from what they would experience in the wild. Lorises that are rescued by the IAR undergo a soft release process, where lorises have the opportunity to forage within an open-top habituation enclosure. While in the enclosure, the IAR staff closely monitors their behavior for several weeks. For staff to be confident about releasing a rescued loris, the loris must show signs of adapting well to foraging, feeding on wild food sources, adequate grooming behavior, and spending most of their time off the ground (IAR, 2021). Lorises that are released following rehabilitation are typically collared and monitored to ensure successful integration into the wild.

The IAR also works to assist local authorities in their efforts to prosecute wildlife criminals. Many wildlife dealers and traffickers operate mainly on social media platforms (IAR, 2021; Gaworecki, 2017), so the IAR has taken initiatives to move their investigative work online. After the confiscation of lorises, the IAR works to publicize this information, resulting in a decrease in loris sales. Market displays of lorises at bird markets and malls in Indonesia are a major driver of loris trade, as the availability of a loris fuels the demand for owning an exotic pet (IAR, 2021; Musing, 2015). In combination with law enforcement support, the IAR has created several conservation programs to educate the local community on the severity of the slow loris trade. Their online platform has successfully asked pet owners to take down videos of slow lorises, and some loris owners have surrendered their pets after learning the implications of the trade and the harmful effects of being kept as pets (IAR, 2021).



Figure 2. Removal of teeth of a slow loris in human care to avoid harm from its venomous bite.

Government of Indonesia

While slow lorises are protected under international, US, and Indonesian laws, the trade and possession of lorises remains commonplace. Under Indonesia's Natural Protection Law, perpetrators of a wildlife crime can face up to 5 years in prison and a 5 million Indonesian Rupiah fine (approximately \$7,400 USD) (Gaworecki, 2017). Selling or owning slow lorises can be prosecuted under Indonesian law, but these laws are not strictly enforced. ProFauna, an organization that works to protect Indonesian wildlife and their habitats, confirmed that lorises are taken from forests to be sold and are not bred in captivity. Investigations and monitoring conducted by ProFauna between 2002 and 2006 confirmed that there were approximately 6,000 – 7,000 lorises caught each year from the wild (ProFauna Indonesia, 2007). Despite efforts from the Forestry Service in Indonesia as well as the Bureau of Conservation and Natural Resources Jakarta to stop the trade of exotic animals, slow lorises are widely available for sale.

Many IAR workers have raised concerns regarding Indonesian law enforcement, stressing that most sellers and owners do not take the wildlife trade laws seriously. Law enforcement officials tend to confiscate animals but rarely prosecute sellers of lorises, which does not deter sellers from continuing the trade (IAR, 2021). The IAR has implemented several educational programs, both online and in person to provide accessible information on the implications of the slow loris trade, but the awareness of the risk to slow loris populations and pet owners does not increase the success rate of prosecuting sellers and owners. Without successful prosecution and sustained efforts to shut down trades, the problem will persist.

U.S. Department of Justice's Environmental and Natural Resource Division (ENRD)

In the United States, the Environmental and Natural Resource Division (ENRD) works to prosecute those who violate US environmental laws (Department of Justice, 2021). The ENRD is

responsible for prosecuting any wildlife trafficking and trade crimes, primarily those under the Endangered Species Act (ESA) and Lacey Act. The purpose of the ESA is to "protect and recover imperiled species and the ecosystem on which they depend" (FWS.gov, 2021). Under the Lacey Act, it is "unlawful to import, export, sell, acquire, or purchase fish, wildlife or plants that are taken, possessed, transported, or sold 1) in violation of U.S. or Indian law, or 2) in interstate or foreign commerce involving any fish, wildlife, or plants taken possessed or sold in violation of State or foreign law" (FWS.gov, 2021). Species of slow lorises that are not considered endangered are not granted protection under the ESA but do have protection from the Lacey Act. Both acts protect endangered species such as the Javan slow loris. The Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) prevents species from becoming endangered or extinct because of international trade (USFWS, 2021). Implementation of CITES can prohibit (Appendix I/III) or regulate (Appendix II/III) trade in listed species based on import, export, or re-export permits (Krishnasamy & Zavagli, 2020). Due to the serious decline in loris populations, all species of slow loris are listed on Appendix I, prohibiting all commercial trade.

Slow lorises can be housed entirely indoors because of their small size, and their trade often goes unnoticed despite protection under the Lacey Act, ESA, and CITES. Most wildlife prosecutions involve large felines that are protected under the ESA, but lorises and other small animals have received little attention, possibly due to their inconspicuous nature. Wildlife crimes are often similar to drug trafficking and other smuggling schemes (justice.gov, 2021). The Department of Justice's official webpage clearly states that "one of the greatest challenges for wildlife prosecutors is to work in the United States, where demand for illegal wildlife is highest, to shut down international suppliers" (justice.gov, 2021). Stopping wildlife trade once animals have entered the country and been distributed to owners is an ongoing issue for law enforcement officers in the United States, stressing a need for greater international support in stopping sellers at the source.

Pet Owners

Slow lorises are desirable as exotic pets due to their resemblance to teddy-bears and small size, but owners often do not recognize the difficulty in housing them (Nekaris et al., 2016). Before they become pets, sellers typically remove the lorises' teeth to prevent their future owner from harm. Sellers rarely use anesthesia to remove loris teeth, causing infections and sometimes death (Kukang, 2021). While owning a loris may be desirable due to their size and appearance, the conditions that lorises face before reaching their owners are inhumane. Owners are typically unaware of these circumstances when purchasing a loris, therefore, the demand persists (Kukang, 2021; Nekaris et al., 2016). Lorises often reach their owners in poor health, due to cramped transport conditions, minimal water, and an unnatural diet (Kukang, 2021) Most loris owners do not understand how to provide proper welfare for these animals, leading to significant health complications.

Owners should provide slow lorises with a healthy diet that promotes a natural weight, as most rescued lorises are overweight and dehydrated (Gaworecki, 2017; IAR, 2021; Nekaris et al., 2016). Without intact teeth, lorises cannot feed on food they would typically find in the wild such as sap and arthropods (Wiens, 2002). This causes owners to feed lorises foods that are high in sugar and easy to consume such as fruit, milk, or rice (Nekaris et al., 2016). When owning lorises, it is important to take into account species-specific dietary requirements to meet basic welfare requirements (Nekaris et al., 2016). As nocturnal animals, slow lorises require dim light conditions to avoid stress brought about from unnatural conditions. Similarly, natural substrates

with hiding spaces that forests provide are necessary to replicate in captive settings to avoid psychological distress (Nekaris et al., 2016). Slow lorises are social primates who interact with other lorises regularly. To achieve proper welfare, owners should house lorises in pairs to support their natural social requirements (Nekaris et al., 2016). Few owners are able to achieve basic welfare for lorises, contributing to their decline in captive settings (Nekaris et al., 2016). However, social media has the ability to communicate educational materials on a large scale and empower communities to make changes (Nekaris et al., 2016). Informing audiences on the complex needs of slow lorises and the implications of improper welfare may dissuade owners from purchasing them (IAR, 2021; Nekaris et al., 2016)

Conservation through Collaboration

The global market for slow lorises continues to thrive despite risks of prosecution and threats to their populations in the wild. The demand for exotic pets is the highest in the United States, suggesting a need for greater intervention here (United States Department of Justice, 2021). The IAR has implemented several educational programs for locals in Indonesia to understand the effects of trading lorises, which have shown some success (IAR, 2021). Several animal rescue groups have worked alongside former sellers, poachers, and hunters to gain a better understanding of how animals are captured and sold. The use of fake social media accounts to act as slow loris buyers may be another way to prosecute sellers, a strategy used by law enforcement for drug trafficking schemes (United States Department of Justice, 2021). These might be valuable strategies for the IAR to implement long-term as an effort to stop trades before lorises are sold as pets.

Decriminalizing the ownership of slow lorises within the United States and working with pet owners to create healthy living conditions for the animals would be a more productive use of law enforcement resources to support the welfare of lorises in captivity. These guidelines should include keeping the lorises' teeth intact, providing dim conditions in the daylight hours due to their nocturnal nature, minimal handling, regular behavioral monitoring, and natural diets. While this solution may seem counterproductive, it would act as a short-term solution to keep populations of lorises healthy both in the wild and in captive settings. For the solution to be successful, it is crucial that the IAR works alongside animal experts to develop a guide that outlines humane living conditions for slow lorises if held in captivity. Following this step, the IAR should collaborate with the Indonesian and U.S. governments to stress the importance of slow loris owners meeting animal care criteria. If these criteria are not met, the owner would be at risk of prosecution for not following animal welfare guidelines under the Animal Welfare Act in the U.S., rather than under the ESA, Lacey Act, or CITES. Under this solution, the ownership of lorises would be legal; however, those who capture and trade lorises would still be vulnerable to prosecution.

To reduce demand for slow lorises, celebrities that have unintentionally driven the trade of lorises could raise awareness about the severity of wildlife trade on natural populations through social media platforms. This would teach loris owners about the impacts of the exotic pet trade, which may lead them to surrender their animals to rescue agencies or create more suitable spaces for them. Celebrities like Lady Gaga and Rihanna have large followings, which would also increase international exposure to this poorly understood topic, and hopefully curb demand for slow lorises as pets. The IAR should continue to raise awareness on the implications of trading exotic animals through educational outreach programs, focusing more on the concerns of slow lorises in human care such as teeth removal, lighting conditions, dietary requirements, etc. to encourage owners to surrender their animals to rescue agencies. These programs should be

directed to locals in Indonesia, but also attempt to reach international audiences through the use of social media.

Conclusion

While often overlooked in law enforcement, the global market for slow lorises has put their populations at risk. In Indonesia, where wildlife laws are not taken seriously and populations of slow lorises are declining (Gaworecki, 2017; Nekaris et al., 2016), a short-term solution of creating adequate living conditions for these animals is critical. Working alongside owners, law enforcement officials and animal care experts should select criteria to ensure the health of lorises in human care in the US, including dim lighting, minimal handling, intact teeth, and regular behavioral monitoring. Long-term, the IAR and the Indonesian government should recruit former sellers, when possible, to learn more about the process of capturing and trading slow lorises. Staff at the IAR should use social media for public outreach to help slow the trade long-term, hopefully stabilizing wild slow loris populations. Aiming to stop trades before lorises cross international borders should remain a priority while providing owners in the United States with concrete guidelines on how to properly care for slow lorises under the Animal Welfare Act. Implementing these suggestions will help prevent the loss of slow loris populations in human care and in the wild.

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