Fall 2017

Boldness and natural behaviors in the African lion (Panthera leo): How are they related?

Courtney M. Kamyk
University of New Hampshire, Durham, ckamyk@gmail.com

Boldness and natural behaviors in the African lion (*Panthera leo*): How are they related?

Courtney Kamyk
IROP
July-August 2017 Livingstone, Zambia

Table of Contents

I. List of Figures

II. List of Tables

III. Acknowledgements

I could not have completed this project without the help of my amazing foreign mentors, Emma Dunston and Jackie Abell, and Drew Conroy, my mentor at the University of New Hampshire. I want to thank Drew especially for pushing me to pursue this project since first semester freshman year and seeing the project through until the end with me.

Special thanks to the African Lion and Environmental Research Trust (ALERT) for allowing me to conduct research at their beautiful Livingstone facility and also to Emma for helping me through data collection and analysis and always making me smile. I also want to thank all the people I met while conducting my research in Africa, especially Dabwiso Sakala, Mulenga Muamba, Kennedy Hiachi, Sara Bylin, Gilbert Daka, Memory Mbeya, Holly Cherise, Charlotte Busetti, Becky Mayer, Baylea Brauner and Emily Drewry. I couldn't have done it without all of your support and laughter.

I also want to thank my mother and father, Sherry and Kevin Kamyk, sister, Hilary, and my grandparents, Dave and Deanna Carlson and Michael Kamyk. Thank you for all of your support physically, mentally, emotionally and most importantly financially. I could not have made my dream of studying lions in Africa come true without all of you.

Lastly, I want to thank my boyfriend, Zackary McPhee, for his constant love and never-ending support.

IV. Abstract

The African lion (*Panthera leo*) population is diminishing rapidly, approximately 43% since 1993 (Bauer et al., 2016. The species is currently listed as vulnerable by the IUCN (Bauer et al., 2016). With numerous threats to current populations including human conflict, prey depletion and habitat loss the African lion is in danger of becoming endangered or even critically endangered in the near future. Ex-situ conservation is a proposed method of restoring populations. The current study focuses on correlations of boldness with natural behaviors and sociality to further understand individual personality in hopes of connecting it with success after reintroduction. Six playbacks were used to assess boldness personality traits of the 12 individuals of the Dambwa pride. Social interactions and daily activity budgets were also recorded. Spearman's correlations were conducted in order to examine correlations between boldness sociality, and average daily activity.

V. Ethical Statement

The research conducted for this thesis was approved by the Institutional Animal Care and Use Committee at the University of New Hampshire in April, 2017 (#170308). All research conducted aimed to provide a comprehensive analysis of personality behavior of the African lion (*Panthera leo*).

The organization this research was conducted in partnership with is known as the African lion and Environmental Trust (ALERT). ALERT has three locations dedicated to the ex-situ rehabilitation of the African lion: Gweru, Zimbabwe; Livingstone, Zambia; and Victoria Falls,

Zimbabwe (ALERT, 2017). The programs are dedicated to the conservation and habitat protection of the African lion (ALERT, 2017). The programs themselves are phase based (ALERT, 2017). The first phase is known as the rehabilitation phase where cubs are born to captive-bred parents are hand raised and taken on human-led walks into natural environments to enable cubs to develop their natural instincts (ALERT, 2017). The second phase is the release phase where lions are released into fenced, managed areas as prides (ALERT, 2017). In this phase lions have the opportunity to function as a wild pride and give birth to cubs that are raised without human interference (ALERT, 2017). The last phase is known as the reintroduction phase (ALERT, 2017). When old enough, cubs from phase two are translocated for reintroduction into appropriate national parks and reserves seeking to restore lost or declining lion populations (ALERT, 2017).

VI. Introduction

Historically, lion populations were once widespread. During the Late Pleistocene, ~12,000 years ago, lions ranged from southern Africa to central America (Barnett et al., 2009). Today's lion populations are now confined to parts of Asia and Africa (Barnett et al., 2009). The lion was previously thought to exist in two distinct subspecies, the Asiatic and the African (Barnett et al., 2014). The International Union for Conservation of Nature (IUCN) has recently proposed a different split—*Panthera leo leo* of Asia and Western, Central and Northern Africa and *Panthera leo melanochaita* from Southern and Eastern Asia—based on research of mitochondrial genomes, microsatellites and autosomal small nuclear polymorphisms (Bauer et al., 2016). Regardless of phylogenetic evolution, the African lion is listed by the IUCN's Red

List as vulnerable. The African lion population has declined approximately 43% over the 21 years from 1993 to 2014 (Bauer et al., 2016). In 1975, populations were at an estimated 200,000 (Myers, 1975), however, by the 1990s it was believed that less than 100,000 remained (Nowell & Jackson, 1996). The most current estimates of lion populations range from 33,000 (Bauer et al., 2016) to 35,000 (Riggio et al., 2013). However, the overall IUCN classification of vulnerable masks an unfortunate dichotomy. Lion subpopulations increased by 12% in four southern African countries (Botswana, Namibia, South Africa and Zimbabwe) and in India, but an observed decline of 60% in sample subpopulations was seen for the remainder of their African range (Bauer et al., 2016). With a rate of decline over 50% in three generations seen in the majority of its range, the lion would meet the IUCN criterion for endangered; a step above vulnerable, but the overall population trend does not meet these limits (Bauer et al., 2016).

Among the causes of decline, the killing in defense of human life and livestock, habitat loss, and prey depletion are among the most detrimental (Becker et al., 2013; Riggio et al., 2013). The main habitat biome utilized by the lion is the savannah (Riggio et al., 2013). Increasing human populations and settlement density and extensive land conversion from wilderness to human-dominated areas threatens natural habitats. In 1960, 11.9 million km^2 of savannahs had fewer than 25 people per km^2 (Riggio et al., 2013). In 2000, only 9.7 million km^2 of savannah had this level of human presence (Riggio et al., 2013). Areas of savannah in Africa with few people have shrunk considerably in the last 50 years and human population projections suggest they will continue to shrink significantly in the next 40 years (Riggio et al., 2013). The current extent of free-ranging lion populations is 3.4 million km^2 or about 25% of available savannah area (Riggio et al., 2013). However, habitats across this area are highly fragmented, leading to additional issues of decreased genetic diversity and an increase in inbreeding. Prey

depletion is partially linked with habitat loss, but more importantly to poaching and the bush-meat trade (Becker et al. 2013). Another emerging threat is canned hunting (Nowak, 2016). In canned hunts lions are captive-bred and hand-raised (Nowak, 2016). These lions are then released into confined spaces within private hunting reserves guaranteeing marksmen an easy target (Nowak, 2016). Canned hunting industry has three means to creating revenue; the revenue earned from tourist volunteers who come to feed and raise the cubs, canned hunts themselves, and trade in lion bones and other body parts for traditional medicine, both within Africa and in Asia (IUCNa, 2006; IUCNb, 2006; Riggio et al. 2013; Nowak, 2016). Furthermore, trophy hunting, when poorly regulated, also contributes to population declines (Packer et al. 2009, 2011; Croes et al. 2011, Rosenblatt et al. 2014). For most species, hunting of male trophy animals can only be detrimental to overall population size when the rate of removal of males is so high that females can no longer be impregnated (Whitman et al., 2004). However, in species where males provide extensive paternal care, such as the lion, the removal of even a few individuals could harm the population as a whole (Whitman et al., 2004). Excessive, unregulated trophy hunting could theoretically cause dominant males to be replaced at such a high rate that associated infanticide with pride take-overs prevents cubs from reaching adulthood and leading to population declines (Whitman et al., 2004). A recent increase in disease transmission has also contributed to population decline (Bauer et al., 2014). The introduction of canine distemper virus in 1994 in lion populations in Tanzania effected almost 85% of the lion population and has since spread to other lion populations throughout central Africa (Roelke-Parker et al., 1996). An introduction of *Mycobacterium tuberculosis* in the cape buffalo (*Syncerus caffer*) in 1990 in South Africa's Kruger National Park has since spilled over into the lion population in the last 15

years (Michel et al., 2006). Approximately 25 lions die per year from tuberculosis (National Geographic, 2017).

Although the exact degree of decline is debatable, it is clear that the African lion population is dwindling and could become severely threatened in the near future if no action is taken. One proposed method of protection is ex-situ conservation, a conservation method in which individuals are raised in captivity and then reintroduced into the wild later in life (Biggins et al., 1999). It is thought that studying animal personalities before release could likely be the key to successful ex-situ reintroduction (Biggins et al., 1999). Animal personality, also known as behavioral syndromes, is a relatively new research area of behavioral ecology. Animal personality is the behavioral responses of an animal across contexts and in different situations (Sih et al., 2004a; Sih et al., 2004b). Animal personality influences social structure and group dynamics (Dunston et al., 2016). One factor known to result in reintroduction failure is that captive raised individuals are behaviorally inept for survival within challenging situations of the wild (Watters & Meehan, 2007). Within animal personality there are personality traits which an individual may or may not express (Reale et al., 2007). Boldness is a personality trait that is particularly important in individual and species survival (Bremner-Harrison et al., 2004). Some research in ex-situ reintroduction programs have assessed boldness as an effective in predictor of post-release survival (Dunston et al., 2016). However, current studies performed on the correlation between boldness and reintroduction success are contradictory. Bremner-Harrison et al. (2004) conducted a study on swift foxes (*Vulpes vulpes*), finding that bolder foxes had higher dispersal and mortality rates than shy foxes post-release. In contrast, Sinn et al. (2014) found that Tasmanian devils (*Sarcophilus harrisii*) that survived post-release were up to 3.5 times bolder than those that did not survive. These mixed results indicate that these responses are species

specific that much more research needs to be conducted to determine the correlation between boldness and re-introductive success across species.

Lions are large carnivores with many threats to their dwindling population numbers. The success of ex-situ reintroduction programs has been largely disputed (Dunston, 2016). Therefore, extensive measures and assessments must be taken to ensure that individuals chosen for release contain appropriate behaviors best suited for survival (Berger-Tal & Saltz, 2016; Dunston, 2016). A recent study by Dunston et al. (2016) conducted research on behavioral phenotypes of African lions (*Panthera leo*) and individual correlations between sociality, boldness and behavior. Research of behavioral syndromes is a relatively new research field and many questions are still unanswered regarding behavioral syndromes (Sih et al., 2004a; Sih et al., 2004b). One especially interesting question that remains is how do behavioral syndromes affect social and ecological dynamics (Sih et al., 2004a; Sih et al., 2004b). This study aims to address how boldness correlates with natural behaviors in African lions, such as resting, aggression, play, and other social behaviors in the Dambwa pride located in Livingstone, Zambia. By studying animal personalities, key species-specific behaviors necessary for survival can be identified allowing for the reintroduction of animals most suited for survival (Watters & Meehan, 2007).

VII. Methods

a. Study Location and Population

The research pride used for this study is known as the Dambwa pride and it is managed by the African Lion and Environmental Research Trust (ALERT). the pride is located within a 707 acre (2.9km^2) fenced reserve within the Dambwa Forest, 8km from Livingstone, Zambia (GPS: S 17°50'31".3' E 25°45'14".2', 900-1000m altitude). Vegetation type of the site consists of

woodland, shrubland and some small grassland areas. The area's climate is -2.8-40.6 °C with 779.8mm of precipitation annually. The pride is composed of six adults and six offspring. The adults were born in captivity in 2008 and were used as walking lions in the Mosi-oa-Tunya National Park in Livingstone, Zambia. They were released into the Dambwa release site in 2011 and allowed to live and reproduce as a natural, wild pride. The first litter of offspring (mother: RS, father: ZU) was born June 30th, 2013 and consists of one male (RS2) and two females (RS1, RS3). The second litter (mother: LE, father: ZU) was born January 30th, 2014 and consists of one female (LE2) and two males (LE1, LE3). During the study impala (*Aepyceros melampus*), puku (*Kobus vardonii*), and duiker (*Cephalophinae*) were available as game species in the release site. The research site when initially constructed also had waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes*) and zebra (*Equus* quagga) available as prey species. It is the intention that these offspring will be released into the wild when old enough, with the females released as a pride and the males as a coalition in a different area to the females to prevent inbreeding.

Data observations took place from June 2nd-August 3rd 2017 during three observation sessions (0800-1100hr, 1230-1400hr, 1430-1600hr).

b. Data Collection

i. Boldness

To determine each lion's boldness, individual reactions to a series of six playbacks were recorded. Two types of playbacks were used: appetitive (n=3) and territorial (n=3). Appetitive playbacks were used to elicit a food response from the pride and consisted of recordings of "hyena on a kill" (*Crocuta crocuta*), "zebra alarm call" (*Equus quagga*), and "African wild dog" (*Lycaon pictus*). The territorial playbacks were used to elicit a territorial response from the pride

and consisted of recordings of "male leopard" (*Panthera pardus*), "unfamiliar lions, mixed sexes", and "four unfamiliar male lions." Both types were utilized to test boldness in both territorial and food specific instances. To ensure that the lions would not become habituated or accustomed to the playbacks, the playbacks were played in a randomly selected order with a minimum of five days between each specific recording Before the playback was started, individual behavior was observed to provide a baseline for each lion. Once the playback was started, reactions of all visible lions were recorded until all behavior of boldness or retreat had ceased and the lions returned to uninterested behavior, such as sleeping or grooming. Observations were recorded for up to 30 minutes after the start of the playback. A scoring system (Table 1), adapted from Dunston et al. (2016), was used to determine boldness scores for individual lions. A +1 score was associated with bold responses such as approach or seeking an elevated position. A -1 score was associated with fearful responses such as retreat or following another pride member. Repetitive bold or fearful behavior resulted in multiple positive or negative scores.

Table 1: Scoring guide used for both appetitive and territorial playbacks.

Category	Did not respond	YES	NO
Observed to hear playback?	0	1	0
Observed to stand in response? (if previously sitting or lying down)	0	1	0
Roared in response	0	1	0
Snarl or have a defensive facial expression?	0	-1	0
Move 5 metres towards playback?	0	1	0
Move 5-10 metres towards playback?	0	1	0
Move 10-20 metres towards playback?	0	1	0
Move 20-50 metres towards playback?	0	1	0
Move >50 metres towards	0	1	0
Number of pauses during approach?	0	1-3 pauses = -1 4-6 pauses = -2 >7 pauses = -3	1
Retreats up to 5 metres from playback	0	-1	0
Retreats 5-10 metres from	0	-1	0
Retreats 10-20 metres from playback?	0	-1	0
Retreats 20-50 metres from playback?	0	-1	0
Retreats >50 metres from	0	-1	0
Number of pauses during retreat?	0	1-3 pauses = 1 4-6 pauses = 2 >7 pauses = 3	0
Retreats behind a physical barrier from playback?	0	-1	0
Seeks a higher position	0	1	0
Sniffs Air	0	1-3 sniffs = 1 4-6 sniffs = 2 >7 sniffs = 3	0
Time Spent Engaged	0	0-5 min = 1 5-10 min = 2 10-15 min = 3 15-20 min = 4 20-25 min = 5 25-30 min = 6 >30 min = 7	0
Follows another pride member?	0	-1	0

ii. Social

To test whether boldness correlates with behaviors, a variety of observation techniques were used. Social interactions were recorded at all-occurrence sampling, with four predetermined interactions recorded: greet, groom, play and aggression. The time, initiator of the interaction, receiver of the interaction, type and whether or not the interaction was accepted was recorded for each observation. A greet was determined as one lion approaching another and rubbing it's head or length of body along the other (Schaller, 1972). Groom interactions were defined as allogrooming, where one individual is licking another (Schaller, 1972). Play behavior was determined as behavior between two individuals with no intent to threaten or harm (Schaller, 1972). In contrast, aggressive behavior was viewed as behavior intended to threaten and harm (Schaller, 1972). Only the first interaction between two individuals was recorded to avoid pseudo replication. A bout was deemed to have ceased when not observed for greater than 1 minute, where upon it was observed again it was recorded as new separate interaction.

iii. Daily activity

An average daily activity budget was composed using a predetermined ethogram (Table 2). Behaviors of all present individuals were recorded for 60 minutes via instantaneous scan sampling every two minutes.

Table 2: Ethogram used to create daily activity budgets.

Abbreviaiton	Behavior
R	Resting
V	Visual (Visually engaged with the surrounding environment)
G	Self-grooming
S	Social (Greet/ Allogrooming /Play /Aggression)
T	Territorial (Roaring/ Scent Marking)
H	Hunting
D	Defication/Urination
E	Eating/Drinking
M	Mating
U	Unseen
AB	Abnormal Behavior (Pacing/ Overgrooming)
L	Locomotion
P	Individual play behavior

c. Data analysis

i. Boldness

At the end of each session, scores were tallied for individuals and a total score was calculated for each playback for each individual lion present. A higher score indicated a lion that was bolder. The playback was played from outside of the release site with a BOSE SLIII speaker system a minimum of 200 m from and out of view of the lions (Dunston et al., 2016). Observations were recorded from within a research vehicle the lions had been previously habituated. In order to analyze results, Microsoft Excel (2017) was used to take the average appetitive score, average territorial score and average overall boldness score for each individual lion. Individual lion boldness scores for each playback are located in Appendix 1.

ii. Social

Social interactions were compiled into the following groups; greet, groom, play, aggression and all social (total number of interactions). For each interaction, a directional pivot table was generated and analyzed using social network analysis program UCINET (Borgatti et al., 2002). UCINET was used to calculate density, degree and betweenness[1] values for each type of interaction (Appendix 2). Indegree measures the amount of interactions an individual receives (Hanneman & Riddle, 2005). In contrast, outdegree measures the number of interactions initiated by an individual (Hanneman & Riddle, 2005). Betweenness measures how central an individual is to the matrix (Hanneman & Riddle, 2005). Due to small sample sizes, data was symmetrized prior to calculation of betweenness. NETDRAW (Borgatti et al., 2002) was then used to generate sociograms for each matrix, providing a visual representation of the interactions observed within the pride for all social, greet, groom, play and aggression.

iii. Daily Activity

Percent of time spent doing each behavior was then calculated for each observation period and used to calculate a total average percentage of time spent doing each behavior, per lion and across the entire pride.

iv. Correlation Assessment

Spearman's rank correlations were conducted using GenStat 17th edition (VSN International, 2014) to assess significance of correlations between boldness, average percentage daily activity and sociality (indegree, outdegree, betweenness).

[1]Betweenness is a term used by UCINET to describe the centrality of an individual to a network.

VIII. Results

a. Sociograms

Nodes represent individual lions, with node shape indicating the sex (square = male, circle = female). The size of the node correlates with the age of the lion, with a smaller node indicating a younger lion, and a larger node indicating an older lion. Lines between nodes represent interactions between lions, with arrows showing the flow of the interaction from initiator to receiver. Line thickness is directly proportionate to the number of interactions observed between lions, with a thicker line indicating more interactions between individuals.

The all pride members were found to be connected to the majority of the pride, with sub-adults LE1, LE2 and LE3 being the least connected. All greet interactions (Figure 2), indicate that all pride members participate in greets. The strongest connections were seen between ZU-KW and RS-LE. Groom interactions (Figure 3) were largely female dominated and were observed most often between RS and LO. Play behavior (Figure 4) largely occurred between sub-adults RS1, RS2, and RS3. Aggression (Figure 5) was observed in ZU, KE, KW, LE1, LE3, RS, RS1, RS2, and RS3 with the strongest connection observed from ZU to RS3. Aggression interactions were not observed for LO, LE and LE2.

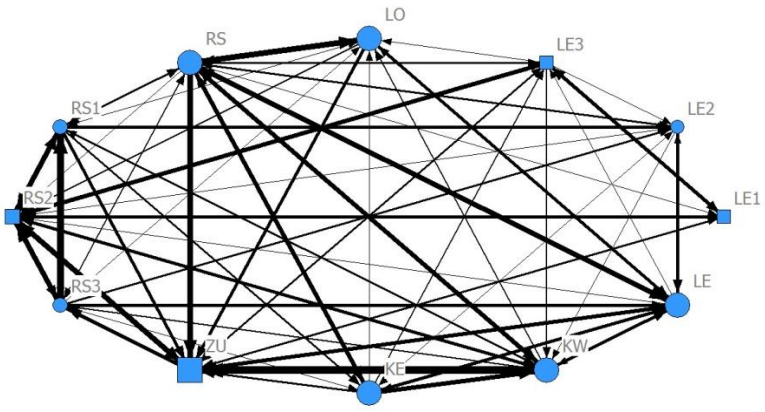

Figure 1: Sociogram of all social interactions between the 12 individuals of the Dambwa pride.

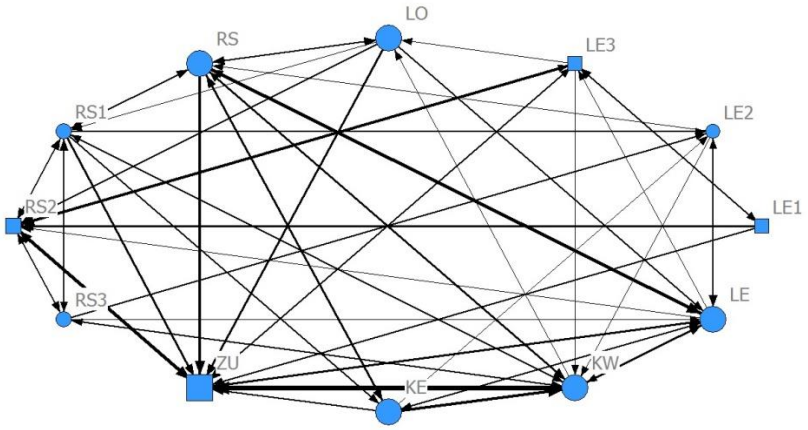

Figure 2: Sociogram of all greet interactions between individuals of the Dambwa pride.

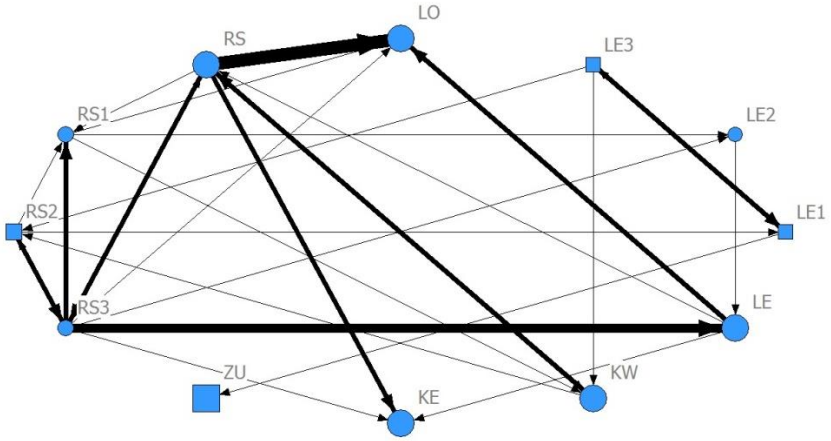

Figure 3: Sociogram depicting all groom interactions between individuals of the Dambwa pride.

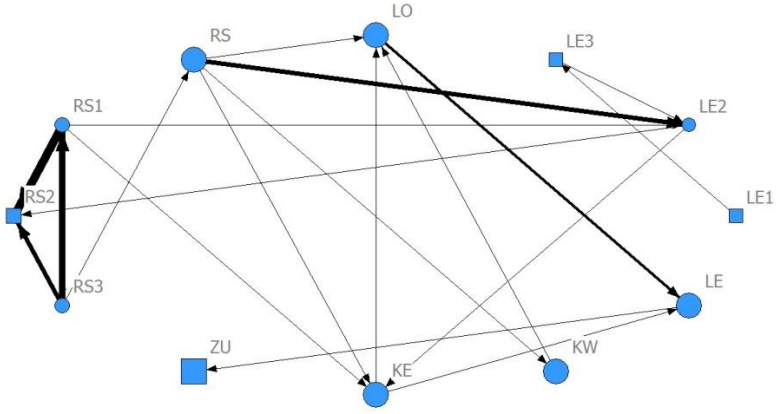

Figure 4: Sociogram of all play interactions between the individuals of the Dambwa pride.

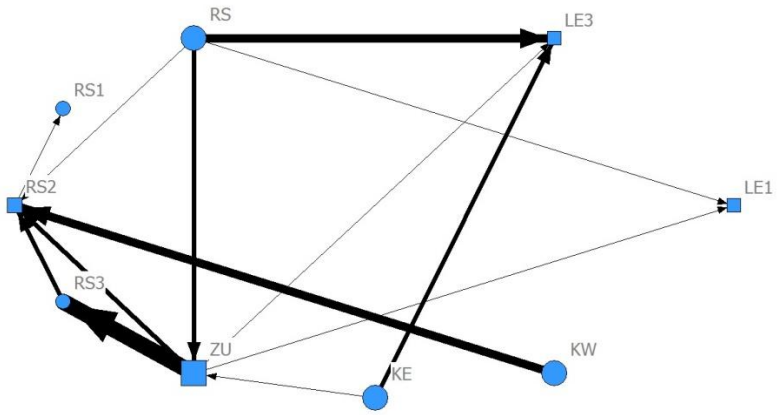

Figure 5: Sociogram of all aggression interactions between members of the Dambwa pride.

b. Boldness

Figure 6 shows the average appetitive boldness scores for the 12 individual lions. The lowest appetitive average was seen in adults KE and ZU (2.33). The highest average appetitive scores are seen in two females, RS1 and LE2, with 5.00 and 5.50 respectively. LE1 was not present for any appetitive playbacks and therefore does not have an associated average appetitive score. The average territorial boldness scores are depicted in Figure 7. The lowest average scores are seen in KE and LE1 (2.00). The highest average territorial scores are seen in two females, RS1 and LE2, with 6.00 and 7.50 respectively. Figure 8 depicts individual average scores for all playbacks. The overall average boldness score for the pride across all playback types was 3.47±1.43.

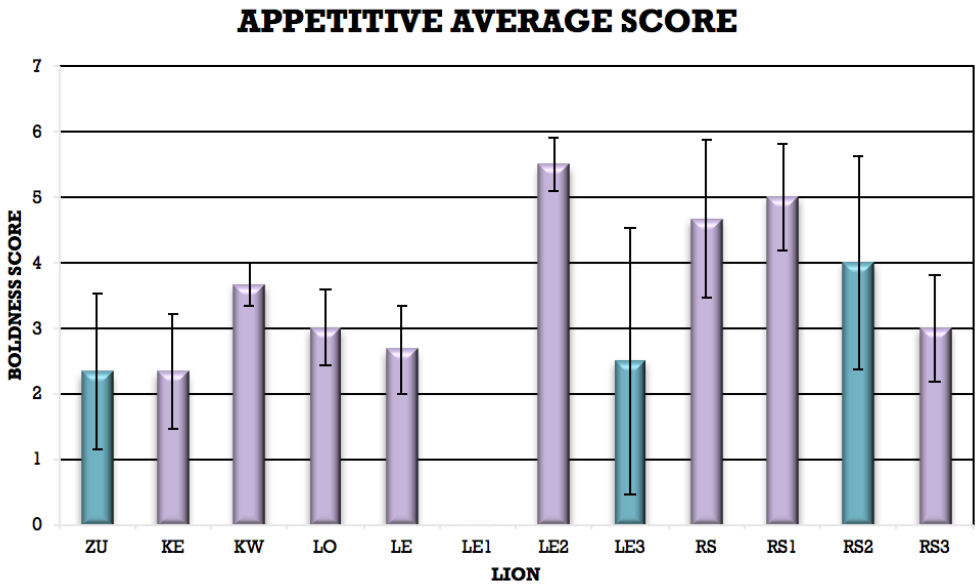

Figure 6: Average appetitive boldness scores for the individual lions of the Dambwa pride. Male lions (ZU, LE1, LE3, RS2) are differentiated with blue bars. Females (KE, KW, LO, LE, LE2, RS, RS 1, RS3) are represented by purple bars.

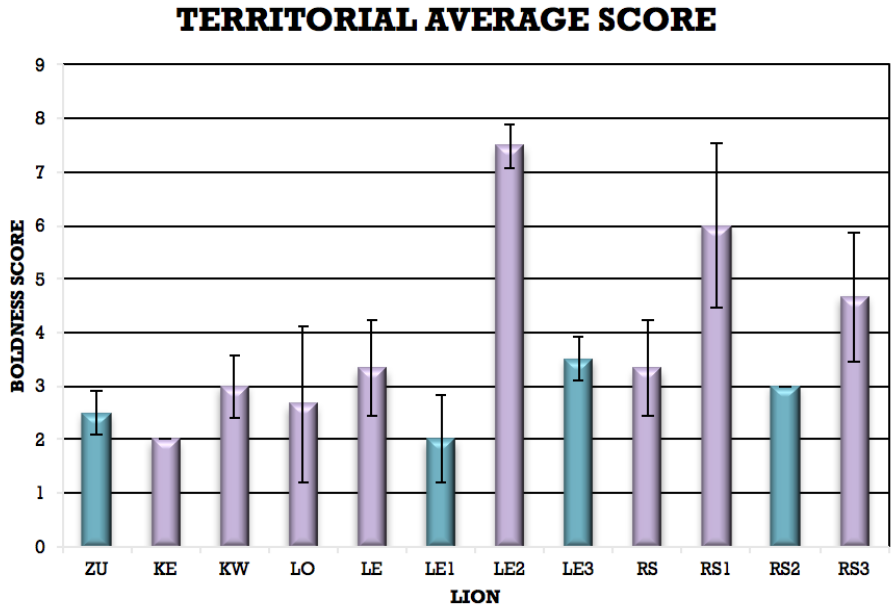

Figure 7: Average territorial boldness scores for the individual lions of the Dambwa pride. Male lions (ZU, LE1, LE3, RS2) are differentiated with blue bars. Females (KE, KW, LO, LE, LE2, RS, RS 1, RS3) are represented by purple bars.

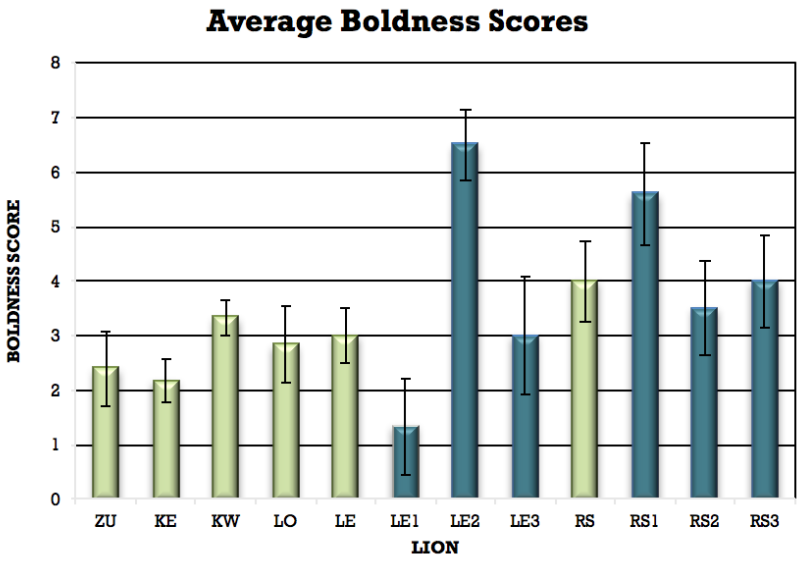

Figure 8: Average boldness scores for all playbacks of the individual lions of the Dambwa pride. Subadults (LE1, LE2, LE3, RS1, RS2, RS3) are differentiated by dark blue bars while adults (ZU, KE, KW, LO, LE, RS) are represented by light green bars.

c. Activity Budget

Pride averages for each behavior are shown in Figure 9 (below). Individual percentages can be found in Appendix 3.

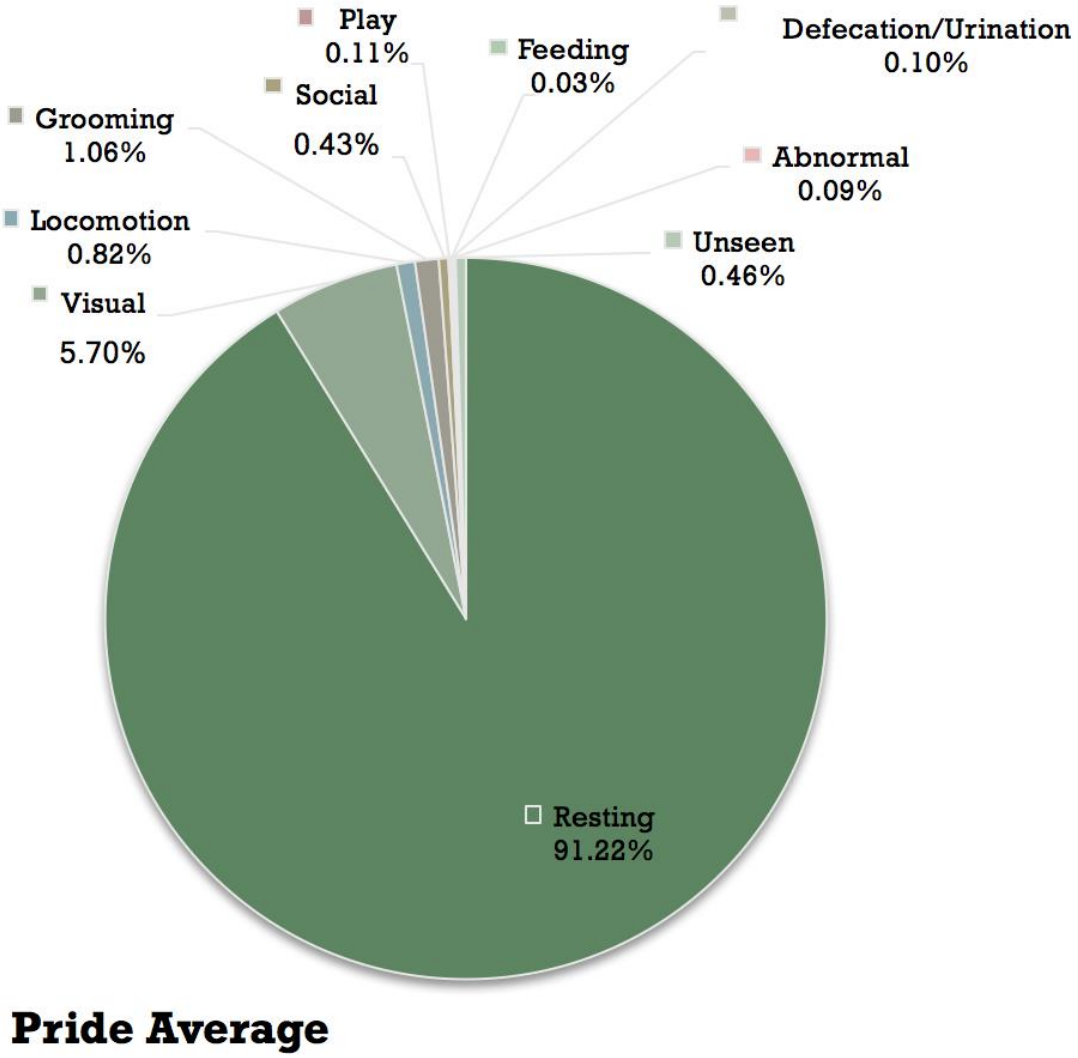

Figure 9: Average daily percentages of behaviors of the Dambwa pride.

d. Spearman's Correlations

Two spearman's correlations were conducted; one for average appetitive boldness (Table 3) scores and another for average territorial boldness scores (Table 4), against social metrics and average percentage daily activity behaviours.

Individuals with higher appetitive scores (Table 3) were overall more social (r_s = 0.585, p = 0.021) and initiated more overall social interactions (r_s = 0.592, p = 0.011). These individuals also initiated more greets (r_s = 0.589, p = 0.011) and groom interactions (r_s = 0.72, p = 0.002). Individuals with high appetitive scores were also more central to the groom network (r_s = 0.594, p = 0.011). Finally, these individuals were less likely to be unseen (r_s = -0.52, p = 0.021), meaning that these individuals were frequently in sight if present during observations.

Lions with high territorial scores (Table 4) were more likely to receive aggressive social interactions from other individuals (r_s = 0.424, p = 0.042). They were also less likely to be observed feeding (r_s = 0.488, p = 0.026). Similar to high appetitive scores, individuals with high boldness scores for territorial playbacks were more central to the groom network (r_s = 0.516, p = 0.021) and more likely to initiate groom interactions with others (r_s = 0.469, p = 0.03). They were also more likely to self-groom (r_s = 0.622, p = 0.008) and exhibit individual play behaviors (r_s = 0.446, p = 0.035). Much like appetitive correlations, territorial individuals were more social (r_s = 0.67, p = 0.005) and less likely to be unseen during activity budgets (r_s = 0.545, p = 0.017).

Table 3: Spearman's correlation results for appetitive boldness scores.

APPETITIVE BOLDNESS TEST		
BEHAVIOR/SOCIAL MATRIX	CORRELATION	P-VALUE
ABNORMAL	-0.131	0.167
AGGRESSION BETWEENNESS	0.307	0.08
AGGRESSION INDEGREE	0.371	0.057
AGGRESSION OUTDEGREE	-0.105	0.183
ALL SOCIAL BETWEENNESS	0.187	0.139
ALL SOCIAL INDEGREE	0.245	0.108
ALL SOCIAL OUTDEGREE	0.592	0.011
DEFECATION	0.332	0.072
FEEDING	-0.358	0.062
GREET BETWEENNESS	0.291	0.089
GREET INDEGREE	0.175	0.143
GREET OUTDEGREE	0.589	0.011
GROOMING	0.377	0.055
GROOM BETWEENNESS	0.594	0.011
GROOM INDEGREE	0.031	0.23
GROOM OUTDEGREE	0.72	0.002
LOCOMOTION	0.152	0.159
PLAY	0.297	0.086
PLAY BETWEENNESS	-0.119	0.175
PLAY INDEGREE	-0.059	0.213
PLAY OUTDEGREE	0.138	0.167
RESTING	0.056	0.213
SOCIAL	0.585	0.012
UNKNOWN	-0.52	0.021
VISUAL	-0.354	0.064

Table 4: Correlation coefficients and p-values for the Spearman's correlation of territorial boldness scores.

TERRITORIAL BOLDNESS TEST		
BEHAVIOR/SOCIAL MATRIX	CORRELATION	P-VALUE
ABNORMAL	0.088	0.196
AGGRESSION BETWEENNESS	0	0.248
AGGRESSION INDEGREE	0.424	0.042
AGGRESSION OUTDEGREE	-0.346	0.067
ALL SOCIAL BETWEENNESS	-0.196	0.132
ALL SOCIAL INDEGREE	-0.108	0.183
ALL SOCIAL OUTDEGREE	0.327	0.072
DEFECATION	0.286	0.089
FEEDING	-0.488	0.026
GREET BETWEENNESS	-0.208	0.23
GREET INDEGREE	-0.383	0.052
GREET OUTDEGREE	0.186	0.139
GROOMING	0.622	0.008
GROOM BETWEENNESS	0.516	0.021
GROOM INDEGREE	0.195	0.132
GROOM OUTDEGREE	0.469	0.03
LOCOMOTION	0.334	0.069
PLAY	0.446	0.035
PLAY BETWEENNESS	-0.202	0.128
PLAY INDEGREE	-0.252	0.104
PLAY OUTDEGREE	0.342	0.067
RESTING	-0.063	0.209
SOCIAL	0.67	0.005
UNKNOWN	-0.545	0.017
VISUAL	-0.053	0.217

IX. Discussion

The aim of this study was to examine how boldness correlated with other behaviors in the African lion (*Panthera leo*) in order to see if boldness could be used as a parameter for

predicting success after reintroduction. Animal personality and behavior is an underutilized resource to conservation management (Greggor et al., 2016). Behavior is an important part of conservation and management because it provides the basis of how animals interact with their environment (Berger-Tal & Saltz, 2016). Ineffective or inappropriate behavior can greatly reduce an animal's fitness in the wild, contribute to the failure of management programs and exacerbate human-wildlife conflict (Berger-Tal & Saltz, 2016). The case is especially true for captive-raised individuals because the environment in which an animal is raised will strongly affect its behavior as an adult (Berger-Tal & Saltz, 2016). These captive-raised animals, if later released into the wild may show maladaptive behaviors if the conditions they were raised in did not adequately prepare them for the wild (Berger-Tal & Saltz, 2016). The concern is that lions raised in captivity may have altered temperaments with maladaptive behaviors, which could lead to a change in how the individual responds to human contact, their hunting abilities, and affect reproductive success (McDougall et al., 2006). Therefore, it is especially important to identify these potential maladaptive behaviors to increase the likelihood reintroduction success of captive-raised individuals.

Behavioral assays of individual's pre-release allow managers to select a more behaviorally, and presumably physiologically and genetically, diverse group intended for release and may serve to increase survival post-release (Merrick & Koprowski, 2017; May, 2016).

Individuals with higher appetitive scores were found to be overall more social and initiated more overall social interactions. They were also found to be more central to the groom network. The correlation seen between these behaviors could be due to the fact that lions observed with high appetitive scores were predominately female. In lion prides, it is well-documented that lionesses are the predominant hunters (Schaller, 1972; Packer et al., 1990). The

results of this study show this trend as well, with females responding more to appetitive playbacks. Previous studies have shown that there is a possible sex bias for grooming, with females more likely to initiate and participate in grooming interactions (Schaller, 1972; Dunston et al., 2016). Therefore, it would be expected that groom interactions would be correlated with high appetitive scores because lions with high scores for these playbacks were mostly female.

Lions with high territorial scores were more likely to receive aggressive social interactions from other individuals. This correlation may be attributed to the fact that RS3, a subadult lion with an average boldness of 4.67 which was above the pride average of 3.47, was the subject of numerous aggressive encounters during observations throughout this study. Similar to high appetitive scores, individuals with high boldness scores for territorial playbacks were more central to the groom network and more likely to initiate groom interactions with others. Much like appetitive correlations, territorial individuals were also more social. As with appetitive playbacks, lionesses were observed to have higher territorial boldness scores over males. This finding was especially interesting due to the fact that male lions in wild prides are typically seen defending territory from competing prides over females (Packer & Pusey, 1997). This could be due to the fact that pride male, ZU, was the same age as the adult females of the pride and raised in captivity alongside them. He naturally became dominant male without ever having to dominate over a pride. Dominant male ZU also may not have considered the playbacks as a threat, as playbacks were conducted often on the pride over the course of many research projects. Lions with high territorial scores were also more likely to self-groom and exhibit individual play behaviors. This could reflect the fact that subadults had high scores for territorial playbacks and are naturally more playful as juveniles. Further application of the acquired data could look into

social dominance positions of individuals and what role they play in other aspects of behavior similar to Dunston et al. (2016).

Personality correlations with boldness obtained in this study can be applied going forward in the ex-situ program (Bremner-Harrison et al., 2004; Sinn et al., 2014; Dunston, 2016; Greenberg & Holekamp, 2017). The subadult lions which were a part of this study will not be released for approximately 1-2 more years. A follow-up study should assess long-term reintroductive success of individuals. Future data can then be analyzed with data similar to the present study to assess whether boldness scores correlate with success after reintroduction.

Studies such as this one in the future could benefit from improved methodology. Due to equipment constraints playbacks for this study were not calibrated to uniform decibel levels. If possible, future studies should use playbacks calibrated to the position of the pride using a microphone and sound level meter similar to the method used by Howard et al. (2008) in prairie mole crickets (*Gryllotalpa major* Saussure). This method would ensure that all responses to the playbacks were due to the calls themselves and not the mere volume of the noise. Due to the nature of this study, data collection occurred over a total of nine weeks only. Future studies could also benefit from an increased sample size, possibly utilizing multiple prides, over a longer study period.

Previous research in different species suggests that boldness may be related to post-release survival (Bremner-Harrison et al., 2004; Sinn et al., 2014; Dunston, 2016; Greenberg & Holekamp, 2017). Similar to swift foxes observed by Bremner-Harrison et al. (2004), a recent study of spotted hyenas found that hyenas who were less bold were significantly more likely to survive to reproductive maturity (Greenberg & Holekamp, 2017). Hyenas are more similar to lions, compared to swift foxes or Tasmanian devils, in that they live in multigenerational social

groups known as clans similar to lion prides (Van Horn et al., 2004). A meta-analysis of boldness conducted by Smith and Blumstein (2008) made the same conclusion; boldness consistently shows a negative correlation with survivorship across species. However, bold individuals had higher reproductive success across species, suggesting a trade-off between survivorship and reproductive success with respect to boldness (Smith & Blumstein, 2008). While the above studies suggest both benefits and drawbacks to boldness as a personality trait in animals it is important to know that these lions have not been released yet. Therefore, no conclusive evidence on boldness correlation with survivorship can be made.

A bachelor thesis conducted during the spring of 2017 by Emma Sopelsa Hall evaluated behavioral responses of the same pride researched in the present study to playbacks of conspecifics with respect to age and sex differences. A series of ten conspecific playbacks of differing sex ratios and number of individuals were used to assess boldness scores of the lion pride (Sopelsa Hall, 2017). Dominant female, Rusha, abbreviated RS in the present study, was found to be the boldest individual of the pride (Sopelsa Hall, 2017). Whereas, in the current study subadult female LE2 was observed to have the highest overall boldness score across all playbacks. Sopelsa Hall (2017) observed subadult female RS3 to have the lowest score. In this study, RS3 was found to have an overall boldness score midrange in the pride. This could be attributed to three factors. The first being the nature of the playbacks used in both studies. Sopelsa Hall (2017) used playbacks exclusively of conspecifics while the present study used playbacks of both conspecifics, prey species, and competitive species. The diversity in playbacks may have led to increased responsiveness of individuals. The second explanation would be that differences in boldness scores reflect the fact that observations of the present study were conducted sometime after the observations of Sopelsa Hall (2017). Subadults may still be

developing their personalities as they age and mature leading to some of the observed variation in boldness scores of the two studies. Differences in observed scores could also be due to the fact that Sopelsa Hall (2017) observed boldness scores of zero for adult all females except RS. All adult females in this study had nonzero values of boldness across all playback types.

With further research coupled with careful monitoring of post-release success of ex-situ individuals, boldness tests of the African lion have the potential to provide a parameter that may be correlated with post-release survival, and subsequently become a critical tool to support future pre-release assessments and program success.

X. References

ALERT | African Lion & Environmental Research Trust - Project Details. (2017). Retrieved December 19, 2017, from http://lionalert.org/alert/project-detail/african-lion-rehabilitation--release-into-the-wild-program

Barnett, R., Shapiro, B., Barnes, I., Ho, S. Y. W., Burger, J., Yamaguchi, N., … Cooper, A. (2009). Phylogeography of lions (Panthera leo ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology, 18*(8), 1668–1677. https://doi.org/10.1111/j.1365-294X.2009.04134.x

Barnett, R., Yamaguchi, N., Shapiro, B., Ho, S.Y., Barnes, I., Sabin, R., Werdelin, L., Cuisin, J. and Larson, G. 2014. Revealing the maternal demographic history of *Panthera leo* using ancient DNA and a spatially explicit genealogical analysis. *BMC Evolutionary Biology* 14: 70. doi: 10.1186/1471-2148-14-70.

Bauer, D., Schiess-Meier, M., Mills, D. r., & Gusset, M. (2014). Using spoor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density. *Canadian Journal of Zoology*, *92*(2), 97–104. https://doi.org/10.1139/cjz-2013-0176

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2016. *Panthera leo*. (errata version published in 2017) The IUCN Red List of Threatened Species 2016: e.T15951A115130419. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en. Downloaded on 01 November 2017.

Becker, M., McRob, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J. and Kakumbi, C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Conservation Biology* 158: 26-36.

Berger-Tal, O., & Saltz, D. (2016). *Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management*. Cambridge University Press.

Biggins, D. E., Vargas, A., Godbey, J. L., & Anderson, S. H. (1999). Influence of prerelease experience on reintroduced black-footed ferrets (Mustela nigripes). *Biological Conservation*, *89*(2), 121–129. https://doi.org/10.1016/S0006-3207(98)00158-X

Borgatti, S.P., Everett, M.G. and Freeman, L.C. 2002. Ucinet for Windows: Software for Social Network Analysis. Harvard.

Bremner-Harrison S, Prodohl PA, Elwood RW (2004) Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (Vulpes velox). Anim Conserv 7:313–320

Croes, B., Funston, P., Rasmussen, G., Buij, R., Saleh, A., Tumenta, P.N. and de Iongh, H.H. 2011. The impact of trophy hunting on lions (*Panthera leo*) and other large carnivores in the Benoué Complex, northern Cameroon. *Biological Conservation* 144: 3064-3072.

Dunston, E. J., Abell, J., Doyle, R. E., Kirk, J., Hilley, V. B., Forsyth, A., ... Freire, R. (2016). An assessment of African lion *Panthera leo* sociality via social network analysis: prerelease monitoring for an ex-situ reintroduction program. *Current Zoology*, zow012. https://doi.org/10.1093/cz/zow012

Dunston, E (2012). The behaviour and welfare of captive African lions (Panthera leo leo) within Australian zoological institutions. Charles Sturt University (11416569).

Greenberg, J. R., & Holekamp, K. E. (2017). Human disturbance affects personality development in a wild carnivore. *Animal Behaviour*, *132*(Supplement C), 303–312. https://doi.org/10.1016/j.anbehav.2017.08.023

Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., … Sutherland, W. J. (2016). Research Priorities from Animal Behaviour for Maximising Conservation Progress. *Trends in Ecology & Evolution*, *31*(12), 953–964. https://doi.org/10.1016/j.tree.2016.09.001

Hanneman, R. A., & Riddle, M. (2005). *Introduction to Social Network Methods*. University of California.

Howard, D. R., Mason, A. C., & Hill, P. S. M. (2008). Hearing and spatial behavior in Gryllotalpa major Saussure (Orthoptera: Gryllotalpidae). *Journal of Experimental Biology*, *211*(22), 3613–3618. https://doi.org/10.1242/jeb.023143

IUCN. 2006a. Conservation strategy for the lion in west and central Africa. IUCN SSC Cat Specialist Group, Gland, Switzerland and Cambridge, UK.

IUCN. 2006b. Conservation strategy for the lion in eastern and southern Africa. IUCN SSC Cat Specialist Group, Gland, Switzerland and Cambridge, UK.

May, T. M. Page, M. J., Fleming, P. A. (2016). Predicting survivors: animal temperament and translocation. Behav. Ecol., 27;969-977.

McDougall, P. T., Réale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation*, *9*(1), 39–48. https://doi.org/10.1111/j.1469-1795.2005.00004.x

Merrick, M. J., & Koprowski, J. L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biological Conservation*, *209*(Supplement C), 34–44. https://doi.org/10.1016/j.biocon.2017.01.021

Michel, A. L., Bengis, R. G., Keet, D. F., Hofmeyr, M., Klerk, L. M. de, Cross, P. C., … Godfroid, J. (2006). Wildlife tuberculosis in South African conservation areas: Implications and challenges. *Veterinary Microbiology, 112*(2), 91–100. https://doi.org/10.1016/j.vetmic.2005.11.035

Myers, N. 1975. The silent savannas. Int. Wildl. 5: 5–10.

National Geographic (2016). Lions of Kruger National Park, South Africa. Retrieved December 4, 2017, from https://news.nationalgeographic.com/news/2005/09/photogalleries/lions/photo2.html

Nowak, K. (2016). The End of 'Canned' Lion Hunting May Be in Sight. National Geographic. Retrieved December 19, 2017, from https://news.nationalgeographic.com/2016/03/140311-trophy-hunting-blood-lions-south-africa-conservation-captive-breeding/

Nowell, K., and Jackson, P. 1996. Wild cats: status survey and conservation action plan. International Union for Conservation of Nature (IUCN), Gland, Switzerland.

Packer, C., Brink, H., Kissui, B. M., Maliti, H., Kushnir, H., and Caro, T. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology* 25(1): 142-153.

Packer, C., Kosmala, M., Cooley, H. S., Brink, H., Pintea, L., Garshelis, D. and Nowell, K. 2009. Sport hunting, predator control and conservation of large carnivores. *PLoS One* 4: e5941.

Packer, C., & Pusey, A. E. (1997). Divided We Fall: Cooperation among Lions. *Scientific American, 276*(5), 52–59.

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why Lions Form Groups: Food is Not Enough. *The American Naturalist, 136*(1), 1–19. https://doi.org/10.1086/285079

Reale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82(2),* 291-318. https://doi.org/10.11116.1469-185X.2007.00010.x

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., … Pimm, S. (2013). The size of savannah Africa: a lion's (Panthera leo) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Roelke-Parker ME, Munson L, Packer C, Kock R, Cleaveland S, Carpenter M, et al. A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). Nature. 1996;379:441–5 10.1038/379441a0

Rosenblatt, E. Becker, M.S., Creel, S., Droge, I., Mweetwa, T., Schuette, P.A., Watson,,F., Merkle, J. and Mwape, H. 2014. Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions. *Biological Conservation* 180: 176-186.

Schaller, G. B. (1972). The Serengeti Lion. The University of Chicago Press.

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology, 79(3),* 241-277. https://doi.org/10.1086/422893

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution, 19(7),* 372-378. https://doi.org/10.1016/j.tree.2004.04.009

Sinn, D. L., Cawthen, L., Jones, S. M., Pukk, C., & Jones, M. E. (2014). Boldness towards novelty and translocation success in captive-raised, orphaned Tasmanian devils. *Zoo Biology, 33(1),* 36-48. https://doi.org/10.1002/zoo.21108

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Sopelsa Hall, E. (2017). *Ex-situ lion conservation: Behavioural responses to playbacks of competitors with focus on sex and age differences*. Retrieved from http://lnu.diva-portal.org/smash/record.jsf?pid=diva2:1134963

Van Horn, R. C., Engh, A. L., Scribner, K. T., Funk, S. M., & Holekamp, K. E. (2004). Behavioural structuring of relatedness in the spotted hyena (Crocuta crocuta) suggests direct fitness benefits of clan-level cooperation. *Molecular Ecology, 13*(2), 449–458. https://doi.org/10.1046/j.1365-294X.2003.02071.x

VSN International (2014) GenStat for Windows. VSN International, Hemel Hempstead

Watters, J. V., & Meehan, C. L. (2007). Different strokes: Can managing behavioral types increase post-release success? *Applied Animal Behaviour Science, 102*(3), 364–379. https://doi.org/10.1016/j.applanim.2006.05.036

Whitman, K., Starfield, A. M., Quadling, H. S., & Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature, 428*(6979), nature02395. https://doi.org/10.1038/nature02395

XI. Appendix

Appendix 1: Individual scores for both appetitive and territorial playbacks. Also depicts appetitive average score, territorial average score and overall average score for each individual. Male lions are highlighted in blue. Females highlighted in red.

	Appetitive Playbacks				Territorial Playbacks				
Lion:	Hyena on a Kill	Zebra Alarm Call	African Wild Dog	Average Appetitive Score	Male Leopard	Unfamiliar Lions, Mixed Sex	Four Unfamiliar Male Lions	Average Territorial Score	OVERALL AVERAGE
KE	1.00	4.00	2.00	2.33	2.00	2.00	2.00	2.00	2.17
KW	4.00	4.00	3.00	3.67	4.00	3.00	2.00	3.00	3.33
LO	4.00	2.00	3.00	3.00	3.00	5.00	0.00	2.67	2.83
LE	2.00	4.00	2.00	2.67	5.00	3.00	2.00	3.33	3.00
LE1	NP	NP	0.00	0.00	NP	1.00	3.00	2.00	1.33
LE2	NP	5.00	6.00	5.50	NP	7.00	8.00	7.50	6.50
LE3	NP	5.00	0.00	2.50	NP	3.00	4.00	3.50	3.00
RS	7.00	4.00	3.00	4.67	3.00	5.00	2.00	3.33	4.00
RS1	NP	6.00	4.00	5.00	3.00	7.00	8.00	6.00	5.60
RS2	NP	6.00	2.00	4.00	NP	3.00	3.00	3.00	3.50
RS3	NP	4.00	2.00	3.00	3.00	4.00	7.00	4.67	4.00
ZU	3.00	4.00	0.00	2.33	3.00	NP	2.00	2.50	2.40

Appendix 2: Indegree, outdegree and betweenness values for all interaction types.

	All Social			Greet			Groom			Play			Aggression		
Lion	Normalized Indegree	Normalized Outdegree	Betweenness Centrality	Normalized Indegree	Normalized Outdegree	Betweenness Centrality	Normalized Indegree	Normalized Outdegree	Betweenness Centrality	Normalized Indegree	Normalized Outdegree	Betweenness Centrality	Normalized Indegree	Normalized Outdegree	Betweenness Centrality
KE	1.182	1.909	1.169	0.545	1.455	0.773	0.364	0	0	0.273	0.182	29.394	0	0.273	0
KW	1.909	2.364	1.371	1.545	1.727	6.621	0.273	0.273	8.485	0.091	0.091	0	0	0.273	0
LE	2.455	1.545	0.884	1.818	1.091	8.091	0.364	0.364	2.727	0.273	0.091	18.182	0	0	0
LE1	0.636	1.091	0	0.182	0.818	0	0.273	0.182	18.182	0	0.091	0	0.182	0	0
LE2	1.182	0.727	0.916	0.545	0.455	1.136	0.182	0.091	0.455	0.455	0.182	39.242	0	0	0
LE3	1.273	1.545	3.232	0.545	1.091	2.788	0.091	0.364	2.727	0.091	0.091	18.182	0.545	0	0.909
LO	1.455	1.273	0.916	0.455	1.091	1.894	0.727	0	0.455	0.273	0.182	8.03	0	0	0
RS	1.818	4.364	5.159	1.364	2.273	1.591	0.364	0.909	9.394	0.091	0.545	21.97	0	0.636	6.364
RS1	1.818	2.455	0.657	0.909	1.455	5.333	0.364	0.273	13.636	0.455	0.727	7.121	0.091	0	0
RS2	3.727	1.727	4.351	1.909	1.182	6.682	0.273	0.364	33.636	0.818	0.091	1.818	0.727	0.091	24.545
RS3	1.364	2.727	0.884	0.455	0.909	1.318	0.364	0.909	24.848	0.091	0.727	3.333	0.455	0.182	0
ZU	4.273	1.364	4.098	3.818	0.545	11.045	0.091	0	0	0.091	0	0	0.273	0.818	20.909

Appendix 3: Average percentages and standard error of all behaviors for all individuals of the Dambwa pride.

	Resting (R)		Visual (V)		Locomotion (L)		Grooming (G)		Social (S)		Play (P)		Hunting (H)	
	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation
KE	94.127	2.132	3.968	1.466	0.159	0.159	0.635	0.293	0.000	0.000	0.000	0.000	0.000	0.000
KW	91.212	3.465	3.939	1.576	0.909	0.324	1.061	0.404	0.303	0.303	0.000	0.000	0.000	0.000
LE	93.333	1.782	5.238	1.292	0.159	0.159	1.111	0.579	0.000	0.000	0.000	0.000	0.000	0.000
LE1	82.917	3.762	10.208	2.536	2.292	1.127	1.667	1.009	1.042	0.845	0.625	0.625	0.000	0.000
LE2	90.159	2.859	6.349	1.750	0.476	0.261	1.111	0.703	0.159	0.159	0.000	0.000	0.000	0.000
LE3	92.222	2.676	4.000	0.987	0.444	0.444	1.333	0.713	1.111	0.901	0.667	0.667	0.000	0.000
LO	92.727	1.651	5.000	1.046	0.909	0.499	1.061	0.459	0.303	0.209	0.000	0.000	0.000	0.000
RS	93.182	1.677	4.697	1.291	0.303	0.209	1.061	0.509	0.758	0.435	0.000	0.000	0.000	0.000
RS1	92.879	2.616	5.152	2.318	0.303	0.209	1.364	0.682	0.303	0.303	0.000	0.000	0.000	0.000
RS2	90.455	2.345	5.909	1.808	2.424	0.855	0.758	0.435	0.455	0.332	0.000	0.000	0.000	0.000
RS3	92.319	1.805	7.917	3.474	1.389	0.693	1.250	0.629	0.417	0.230	0.000	0.000	0.000	0.000
ZU	92.576	2.045	6.212	1.865	0.152	0.152	0.303	0.209	0.303	0.209	0.000	0.000	0.000	0.000
	Eating/Drinking (E)		Mating (M)		Urination/Defication (D)		Territorial (T)		Abnormal (AB)		Unseen (U)			
	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation	Average (%)	Standard Deviation		
KE	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.111	1.111		
KW	0.000	0.000	0.000	0.000	0.758	0.758	0.000	0.000	0.000	0.000	1.818	1.818		
LE	0.159	0.159	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
LE1	0.000	0.000	0.000	0.000	0.208	0.208	0.000	0.000	1.042	1.042	0.000	0.000		
LE2	0.159	0.159	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.587	1.587		
LE3	0.000	0.000	0.000	0.000	0.222	0.222	0.000	0.000	0.000	0.000	0.000	0.000		
LO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
RS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
RS1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
RS2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
RS3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.556	0.556		
ZU	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.455	0.455		