



# The Relationship Between the Lion's (*Panthera Leo*) Boldness and Other Behaviors

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## Abstract

A reduction of 43% in the African lion (*Panthera Leo*) population since 1993 has led to its classification as vulnerable by the IUCN. Contributing factors include decreased prey availability, habitat degradation, and human conflict, highlighting the need for effective conservation strategies. Ex-situ conservation is emerging as a potential solution, aiming to understand personality traits like boldness in lions and their implications for successful reintroduction. This research focuses on evaluating the boldness levels of the Dambwa pride's twelve members through six playbacks, analyzing their social interactions and daily activities. Furthermore, it emphasizes the importance of behavioral competence in lions being reintroduced to the wild, advocating for thorough pre-release assessments to ensure their viability. The research also presents the first comprehensive analysis of lion prides originating from captivity and their interactions with a wild pride, providing insights into how captive histories may influence behavior. Evaluation of various behavioral facets such as social interactions and hunting patterns revealed differences in daily activity between sexes, with adults generally sleeping more than cubs. Social network analysis (SNA) further helped compare pride behaviors at individual and subgroup levels, illustrating social cohesion within prides and highlighting the role of age subgroups and keystone adult females. Additionally, territorial assessments showed how central territories reflect resource usage and needs, underscoring the complexity of lion social dynamics and conservation efforts.

**Keywords:** African lion, *Panthera*, resource utilization, behavior

## Introduction

Behavior is a leading sign of anthropogenic disruptions or population health concerns; therefore, management strategies should revolve around altering it. Furthermore, environmental changes may have an immediate impact on animal behavior, in contrast to population density. What role does knowledge of an animal's habits have in protecting it? The answer may change according to the species in question, but it does have far-reaching implications for how we try to protect rare and endangered species. Thus, the conceptual framework may aid in the formation of the scientific investigation of a threatened species and provide new management concerns. For instance, the geographical and temporal components of population censuses are impacted by ranging habits, breeding periods, and locations; so, behavioral information indirectly influences conservation and monitoring tactics. In the field of conservation biology, prior research has shown that organisms' behavioral reactions to changes in their

environment are effective leading indicators because of how quickly they occur. Due to scientific and cultural barriers as well as historical ones, the connection between conservation biology and animal behavior is tenuous at best.

Understanding animal behavior and how it relates to conservation biology is something that has recently attracted a lot of attention. This fact undergirds current literature that suggests a shift toward merging conservation biology with animal behavior. For instance, in order to contribute to conservation biology, a number of behavioral biologists have written books and reviews discussing the significance of animal behavior and its role in the field. Conservation biologists may struggle to see how behavioral information might aid in solving practical conservation challenges in the absence of a well-defined conceptual framework for such integration. For instance, if behavioral research were to supersede conservation efforts, the field would require a shift in focus and the addition of additional experts to its interface. The most critical thing is that it should zero in on

the parts of animal behavior that might affect essential rates or make them more vulnerable to human manipulation or interference. Both experimental and observational methods are necessary for a thorough understanding of animal behavior. We need to see a behavior in its natural environment and in its whole before we can hope to grasp it. By breaking down a pattern or sequence of behaviors into its component parts, we may better understand how they work in relation to the animal's physical and biological surroundings. Drawing on this body of information, we may conjecture about the behavior's purpose and the variables that influence it, as well as form our own opinions about it. We may formulate testable hypotheses in the scientific language. These are well-posed topics that we want to address via well-planned studies that track and alter certain aspects of behavioral performances. The outcomes of these kinds of investigations and observations will be taken into account throughout this book.

There are two main levels that may be used to study animal behavior. What causes an action to take place might pique our curiosity at the physiological level. To clarify, I'm asking how a certain behavior emerges from the interplay of an animal's biochemistry, nervous system, muscles, and senses. But concerns about the animal as a whole and its environment are just as intriguing. At this level, we can think about how an animal's social experiences, its larger ecosystem, or the environment impact its behavior. In order to conduct this kind of whole animal observation, researchers may go out into the field and observe the animals in their natural habitat, or they could bring the animals into a controlled laboratory setting.

It is now usual practice to conduct experimental manipulations in the field and "field" simulations in the lab, suggesting that these lines have begun to blur. The introduction of powerful but user-friendly computers, however, must be considered the most noteworthy breakthrough in the field of animal behavior research in recent times. At a fraction of the expense of more conventional methods, computer models allow us to mimic behavior and conduct and assess "experiments" without involving any animals (apart from the human operator). Though helpful, this method cannot substitute in-person observations of real animals since any model is only as accurate as the data fed into it.

### Literature Review

Rahman, Tawfiqur *et al.* (2022) <sup>[1]</sup>. This article examines how changes in behavior, often instigated by environmental disruptions, can trigger a ripple effect throughout species interactions, which are essential to ecosystems. It investigates the transmission of behavioral responses among interconnected species and the resulting ecological consequences. The authors argue that modifications in these interactions can influence ecosystem structure and function, affecting aspects such as biodiversity, stability, and ecosystem services. They propose a theoretical framework that links behavioral alterations to shifts in species interactions and community dynamics, emphasizing the importance of focusing on particular species whose behavioral adaptations significantly affect ecological processes. A thorough understanding of these responses and their underlying drivers is vital for assessing human impacts

on ecosystems. The article highlights the critical role of species interactions in sustaining biodiversity and ecosystem functionality, asserting that the insights gained may enable predictions of the effects of ongoing disturbances and inform strategies for mitigating such impacts.

Nelson, Ximena (2014) <sup>[2]</sup>. *Emerging Discipline of Conservation Behavior: On the Verge of Success or Unattainable Ideal?* Discusses the intersection of behavioral ecology and conservation biology, emphasizing the importance of understanding animal behavior for successful conservation. Knowledge of species' home ranges, food sources, mating systems, and dispersal mechanisms is crucial for reintroductions and establishing corridors. The paper highlights the roles of species in ecosystems and the need to recognize those with critical ecological functions, especially amid extinction threats. Despite recognizing the need for collaboration, behavioral ecologists often engage slowly with conservation biologists. The author, a behavioral ecologist, researches the extent of this collaboration by analyzing academic literature from 1983 to 2013 and finds an increase in involvement in conservation biology, indicating its growing significance. The text advocates for closer ties between the two fields, asserting that such collaboration is essential for effective conservation practices and understanding ecological dynamics.

Hale, Robin *et al.* (2020) <sup>[3]</sup>. Efforts to restore damaged habitats are crucial for enhancing biodiversity, yet achieving self-sustaining populations of targeted species remains challenging. Understanding factors that impede restoration progress and developing strategies to overcome these limitations is essential. This document reviews literature emphasizing the importance of animal behavior in planning restoration projects, particularly when species fail to colonize rehabilitated areas or when habitat characteristics do not meet their needs. A decision tree framework is provided for management agencies facing budget constraints on behavioral data collection, highlighting instances where such data is beneficial. Gaps in knowledge about animal behavior are discussed, along with potential pathways to improve biodiversity restoration outcomes. While restoration initiatives can mitigate some negative impacts of habitat degradation, they are not always optimal for targeted species. A deeper understanding of animal behavior can enhance restoration program design and evaluation, promoting better collaboration between practitioners and behavioral ecologists to refine restoration strategies.

Buchholz, Richard *et al.* (2019) <sup>[4]</sup>. This review highlights the role of behavioral features in animals' adaptation to climate change, arguing that simply addressing temperature rise is inadequate for survival in the Anthropocene. It calls for integrative and applied behavioral research to enhance our understanding of how animals cope with extreme weather events. Starting with a fictional ground squirrel's thermoregulatory behavior, the analysis considers scenarios such as behavioral plasticity and adaptation. The framework proposed categorizes extreme events (heat waves, storms, floods, wildfires, droughts) as major selection pressures shaping behavior. Examples of adaptations from species in harsh climates are provided. Methodological recommendations for studying behavioral responses to climate change are also outlined. The review concludes by

advocating for a public video archive and citizen science initiatives to increase awareness and support conservation efforts, focusing on species preservation and informed habitat management amidst biodiversity threats from climate change.

Dimitri, Lindsay *et al.* (2018) [5]. Down Below emphasizes the need for natural resource managers to recognize species-specific behavioral differences in wildlife management. It argues that understanding individual behaviors can enhance long-term management strategies. Four examples are cited: First, analyzing livestock foraging behaviors is essential for improving efficiency and output. Second, effective management of declining sage-grouse populations requires knowledge of their mating, nesting, and migratory behaviors. Third, insights into mountain lion predation patterns, including prey switching from mule deer to bighorn sheep or wild horses, are crucial for effective management and expenditure allocation. Lastly, the scatter-hoarding behaviour of granivorous mice supports seedling recruitment, linking animal behavior to conservation. The document concludes by advocating for a nuanced understanding of animal behavior to improve wildlife management and enhance species conservation and ecosystem health.

## Materials and Methods

The observations were carried out between one and three times daily, according to the periods mentioned before, for every pride. Data was taken directly from a study vehicle during observation sessions, which lasted at least one hour but might go up to three or four. Prior to data collection, all prides were acclimated to the study vehicles.

**Social interactions:** During each observation session, we meticulously documented every single social contact that we saw. Social interaction kinds, as outlined by Schaller (1972) [11], were arranged in a table (Table 1). Whether the recipient accepted, disregarded, or refused the engagement, as well as the kind of interaction and the individuals involved in initiating and receiving it, were documented. Once the behavior was no longer seen for 1 minute, the social interaction session ended. A new bout was recorded if the behavior was witnessed again after this interval had elapsed. The first kind of contact between the two people was documented, and after a minute had passed without interaction, the following behaviors were recorded. Data acquired on the Makhutswi 2 pride and the Dambwa pride after December 6, 2014, are not included in the analysis presented in this dissertation.

**Table 1:** Categories and descriptions of social interaction behaviors

Measure	Description
Greet	An individual was observed to make contact with another pride member(s), either by head-to-head or head to body contact.
Social Grooming	An individual was observed to lick another pride member(s).
Social Play	An individual was observed to interact with another pride member(s) in a playful manner, categorised into four types as described by Schaller (1972) [11]
Chase	An individual pursues another, and can include a lion attempting to jump on the back of the leading lion.
Wrestle	An individual lies on their back while another stands, crouches or lies, mauling the throat or grasping a paw or other part of the body with their mouth.
Pawing	An individual gently swats at another with their forepaw.
Stalk	An individual crouches, pauses and advances in a stalk or crouched walk, which can fasten into a rushed approach, towards a target pride member.
Aggression	An individual was observed to exhibit any of the following in response to the presence of another pride member(s); protective stance, snarl, aggressive vocalisation, unfriendly swipe with the front paw, retreat, aggressive chase or wrestle.

## Hunting behaviour

During the observation sessions, hunting behavior was documented at every instance. The following details were documented: the kind of vegetation, the prey species, the lion(s) that started and continued the hunt, the approach type (flank left, right, or straight), if a pursuit was started, a kill was made, and who consumed the corpse. The pride members who displayed physical indications of feeding, such as an expanded stomach or blood on the face and forelimbs, were documented along with the type of prey if it could be identified, in cases where the pursuit and kill were not seen.

## Boldness test

At the conclusion of an afternoon observation session, which lasted from 1600 to 1800 hours, participants were asked to demonstrate their level of boldness. A group of unknown lions (about eight in number) and a clan of spotted hyenas (about four in number) were used as a stimulus, with the vocalizations of these animals serving as a reminder of their territorial and feeding roles, respectively. There was a 180-second lion replay and a 220-second hyena recording.

## Data Analysis

### Social

We categorized people's social interactions as follows: aggressive, play, greet, groom, and all social. Using the social network analysis application UCINET, each interaction was assessed using a directional pivot table (Borgatti *et al.*, 2002) [12]. Degree, betweenness, density values for each interaction type were calculated using UCINET. The number of interactions that a person gets is measured by indegree (Hanneman & Riddle, 2005) [13]. Outdegree, on the other hand, counts how many encounters a person initiates (Hanneman & Riddle, 2005) [13]. According to Hanneman and Riddle (2005) [13], betweenness is a measure of how important a person is to the matrix. Data was symmetrized before betweenness was calculated because of tiny sample numbers. Next, sociograms were created for each matrix using NETDRAW (Borgatti *et al.*, 2002) [12]. These sociograms show the interactions inside the pride for each of the following categories: Social, greet, groom, play, and aggressive. Using a battery of observational tests, we looked for evidence of a relationship between boldness and actions.

The four preset social interactions greet, groom, play, and aggression were recorded during all-occurrence sampling. At the time of each observation, we noted the sort of contact, the recipient, the one who initiated it, and whether or not it was accepted. As a lion approach another and brushes its head or body against it, it is said to be greeting each other (Schaller, 1972) [11]. Allogrooming, in which one person licks another, was once considered a groom interaction (Schaller, 1972) [11]. Interactions between people were defined as play when neither one was intentionally trying to hurt the other (Schaller, 1972) [11]. Aggression, on the other hand, was defined as actions taken with the intent to cause injury or threat (Schaller, 1972) [11]. To prevent the possibility of spurious replication, we only recorded the first encounter between each person. After more than one minute had passed without observation, the bout was considered to have ended; further observations were recorded as new interactions.

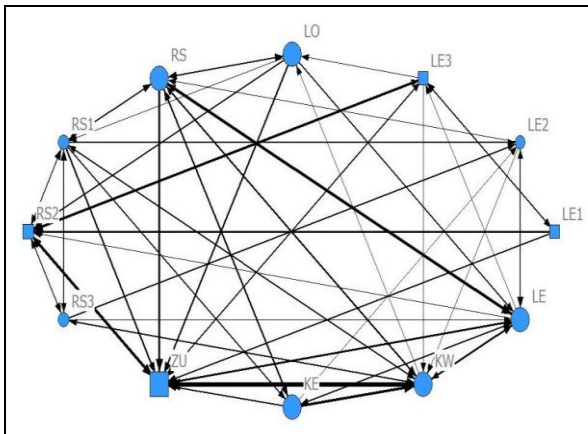
**Correlation Assessment**

This study used Spearman's rank correlations in GenStat 17th edition to evaluate the significance of the correlations between boldness, average% daily activity, and sociality (indegree, outdegree, betweenness) (VSN International, 2014).

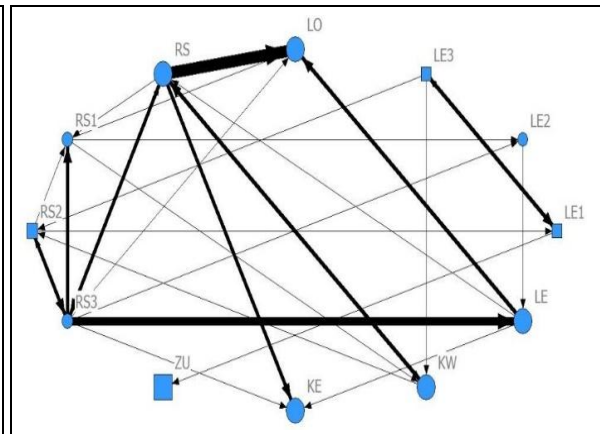
**Results and Discussion**

**Boldness and natural behaviors in the African lion (Panthera Leo)**

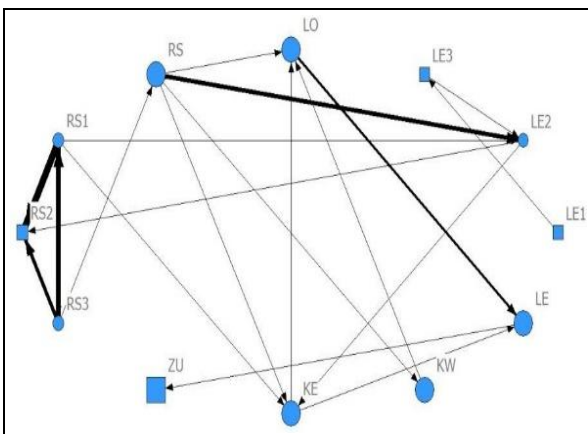
**Sociograms:** The sex of a lion is indicated by the form of its node; a square denotes a male lion and a circle a female. Based on the size of the node, which is proportional to the lion's age, a smaller node denotes a younger lion and a larger node an older lion. Arrows illustrate the path of the connection from its source to its receiver, whereas a line connecting two nodes shows an interaction between two lions. More interactions between persons are represented by a thicker line, and the number of interactions is directly proportional to the line's thickness. The weakest links were found in sub adults LE1, LE2, and LE3, although it was found that all members of the pride were linked to the majority of the pride. According to every encounter, every member of the pride greets each other. The strongest connections were found between ZU-KW and RS-LE. During groom contacts, which mostly happened between RS and LO, females were more common. It was mostly the sub adults RS1, RS2, and RS3 that were playing. The following areas were recognised for hostile behaviour: ZU, KE, KW, LE1, LE3, RS, RS1, RS2, and RS3. The highest correlation was seen between ZU and RS3. Neither LO nor LE nor LE2 shown any aggressive interactions.



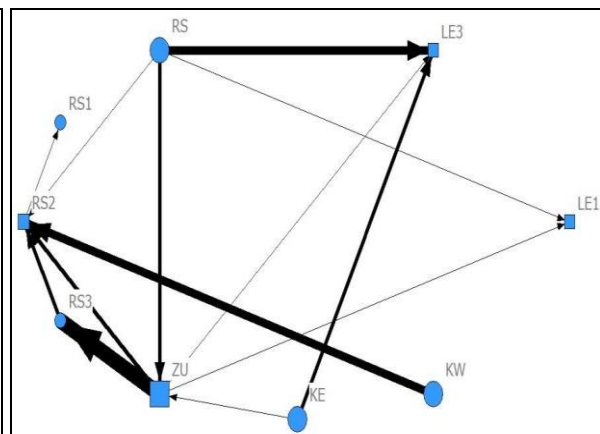
**Fig 1:** Sociogram of all greet interactions between individuals of the Dambwa pride



**Fig 2:** Sociogram depicting all groom interactions between individuals of the Dambwa pride



**Fig 3:** Sociogram of all play interactions between the individuals of the Dambwa pride

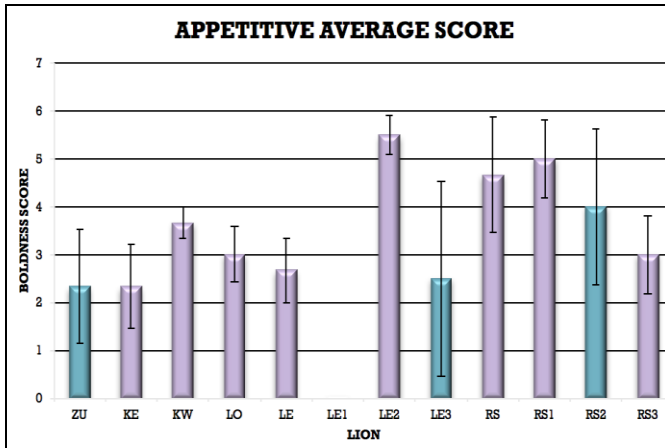


**Fig 4:** Sociogram of all aggression interactions between members of the Dambwa pride

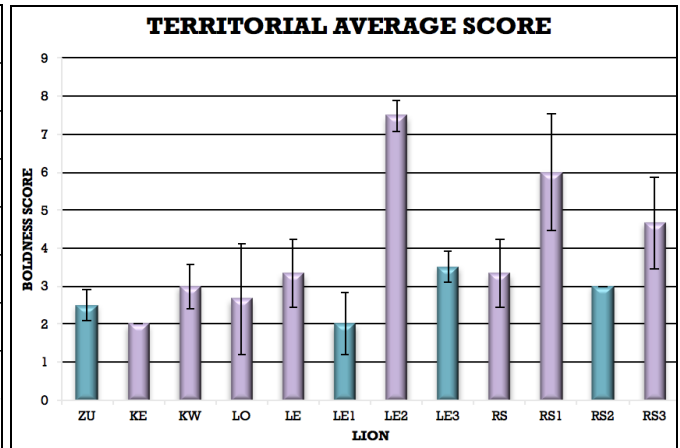
**Boldness**

You can see the twelve lions' average scores for appetitive boldness in Figure 6. The average hunger level was 2.33 among adults KE and ZU. With an average of 5.00 and 5.50, respectively, RS1 and LE2 are the two females with the highest average appetitive scores. There is no average appetitive score for LE1 since it was not included in any

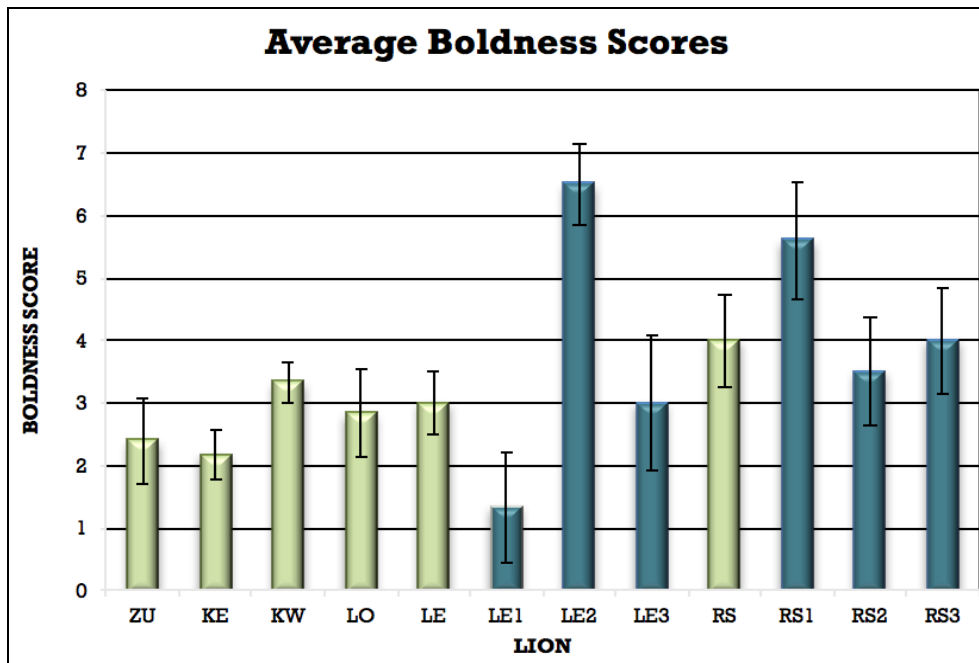
appetitive playbacks. See Figure 7 for the mean territorial boldness scores. Both KE and LE1 had the lowest average scores, coming in at 2.00. One female (RS1) and one male (LE2) had the highest average territorial scores (6.00 and 7.50, respectively). Figure 7 shows the average scores for each playback as an individual. The pride has an average boldness score of  $3.47 \pm 1.43$  across all modes of listening.



**Fig 5:** Individual lions' average ratings for appetitive boldness in the Dambwa pride. You can tell the male lions apart (ZU, LE1, LE3, RS2) by studying the blue bands. The females are shown by the purple bars: KE, KW, LO, LE, LE2, RS, RS 1, and RS 3



**Fig 6:** Averaging the lions' territorial boldness ratings from the Dambwa pride. You can tell the male lions apart (RS2, LE1, and ZU) may be learnt by observing the blue bands. We can see the ladies represented by the purple bars: KE, KW, LO, LE, LE2, RS, and RS 1. RS 3



**Fig 7:** The average boldness ratings for each lion in the Dambwa pride over all of their playbacks. Light green bars indicate adults (ZU, KE, KW, LO, LE, RS), while dark blue bars denote subadults (LE1, LE2, LE3, RS1, RS2, RS3)

**Activity Budget**

Figure 8 exhibits the average pride for each behavior, as

may be seen below. The percentages for each item are detailed in Appendix 3.

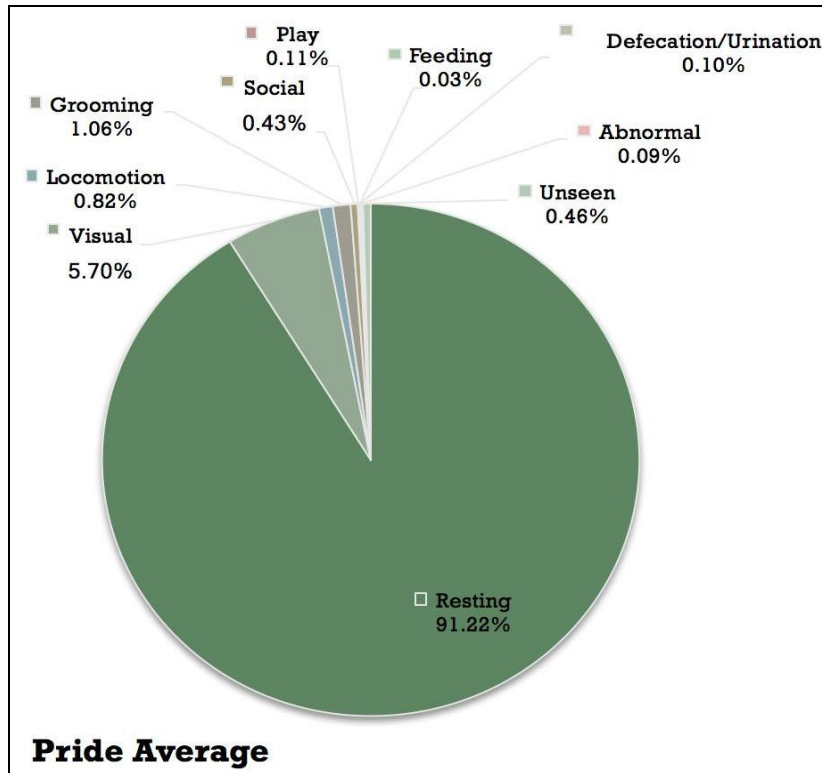


Fig 8: Average daily percentages of behaviors of the Dambwa pride

**Spearman’s Correlations**

Table 2 presents findings linking social indicators and daily activity behaviors with Spearman's correlations and boldness scores. Key results show that higher hunger scores correlate positively with extroversion ( $r_s=0.585$ ,  $p=0.021$ ) and a propensity for initiating conversations ( $r_s=0.592$ ,  $p=0.011$ ). Significant grooming behaviors are associated

with individuals scoring well on appetite ( $r_s=0.594$ ,  $p=0.011$ ) and those from territorial regions exhibit more hostile social interactions ( $r_s=0.424$ ,  $p=0.042$ ). Additionally, higher boldness scores are linked to increased self-grooming ( $r_s=0.622$ ,  $p=0.008$ ) and greater overall social behavior ( $r_s=0.67$ ,  $p=0.005$ ), highlighting the interconnectedness of appetitive and territorial boldness.

Table 2: Spearman’s correlation results for appetitive boldness scores

Appetitive boldness test		
Behaviour/social matrix	Correlation	P-Value
Abnormal	-0.131	0.167
Aggression Betweenness	0.307	0.080
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	0.230
Groom Outdegree	0.720	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	-0.520	0.021
Visual	-0.354	0.064

**Table 3:** Scores for territorial boldness and their corresponding Spearman's correlation coefficients and p-values

Territorial boldness test		
Behavior/social matrix	Correlation	P-value
Abnormal	0.088	0.196
Aggression Betweenness	0.000	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	0.230
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	0.030
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	0.670	0.005
Unknown	-0.545	0.017
Visual	-0.053	0.217

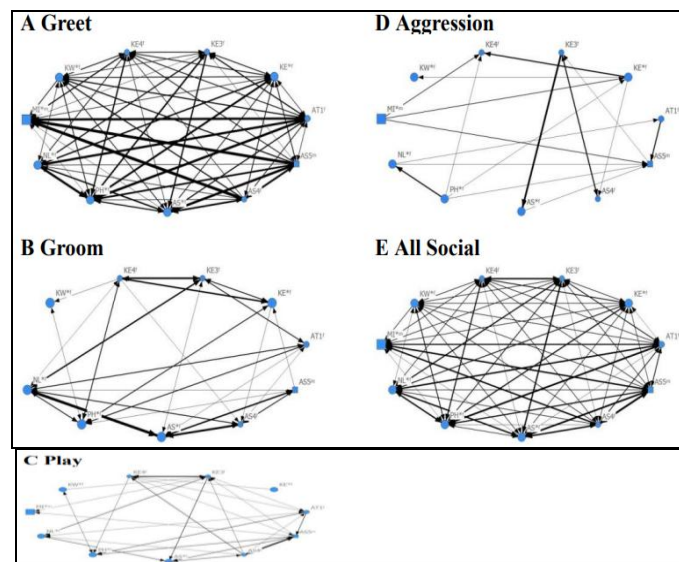
**Exploring African Lion (*Panthera Leo*) behavior phenotypes**

**Activity budget:** That resting behaviors accounted for an average of 60.91% of the total time examined, with a range of 51.69% (MI\*m) to 68.98% (KE\*f), where \* denotes captive-origin. An average of 16.62% pride was observed, with alert behaviors ranging from 24.22% (KE4) to 8.51% (MI\*m). The findings indicate that sub-adults exhibited a positive correlation between alert behaviours and age ( $r=0.928$ ,  $N=11$ ,  $p<0.001$ ). Exhibited higher alertness levels than adults. A substantial relationship between session duration and pride behavior was seen. During session 2, which lasted from 1100 to 1300 hours, the resting behavior peaked at 70.94%, in contrast to sessions 1 and 3, which

lasted from 0630 to 0830 hours and 1600 to 1800 hours, respectively, with a significant difference  $p<0.001$  when comparing the three time periods ( $F_{2,20}=45.573$ ).

**Social interactions**

Pride was significantly related to all social density indicators (0.909) and greet (0.818). Density was low for the other networks, suggesting that some nodes were partially linked (groom=0.409, play=0.309, hostility=0.164). All members of the pride were linked, according to the Sociograms for the adult male MI and adult female NL, as well as all other social networks. Table 4. shows that these two people have low Betweenness centrality ratings, and they aren't very active in the all-social network cliques.



**Fig 9:** Network diagrams derived from social interactions

Each lion is represented by a symbol, which is a node. The form of the node indicates the sex of the representation of lions use circles for females and squares for males, with node size directly correlating to the lion's age (bigger symbol=older lion). A thicker line between dyads implies a larger frequency of interaction, which is proportional to the

intensity of link between a pair of lions. All four cliques had lions that were important to the greet network (Table 4). This network did not include any adult male myocardial infarction and both adult females KW and adult male MI had low centrality (Table 4).

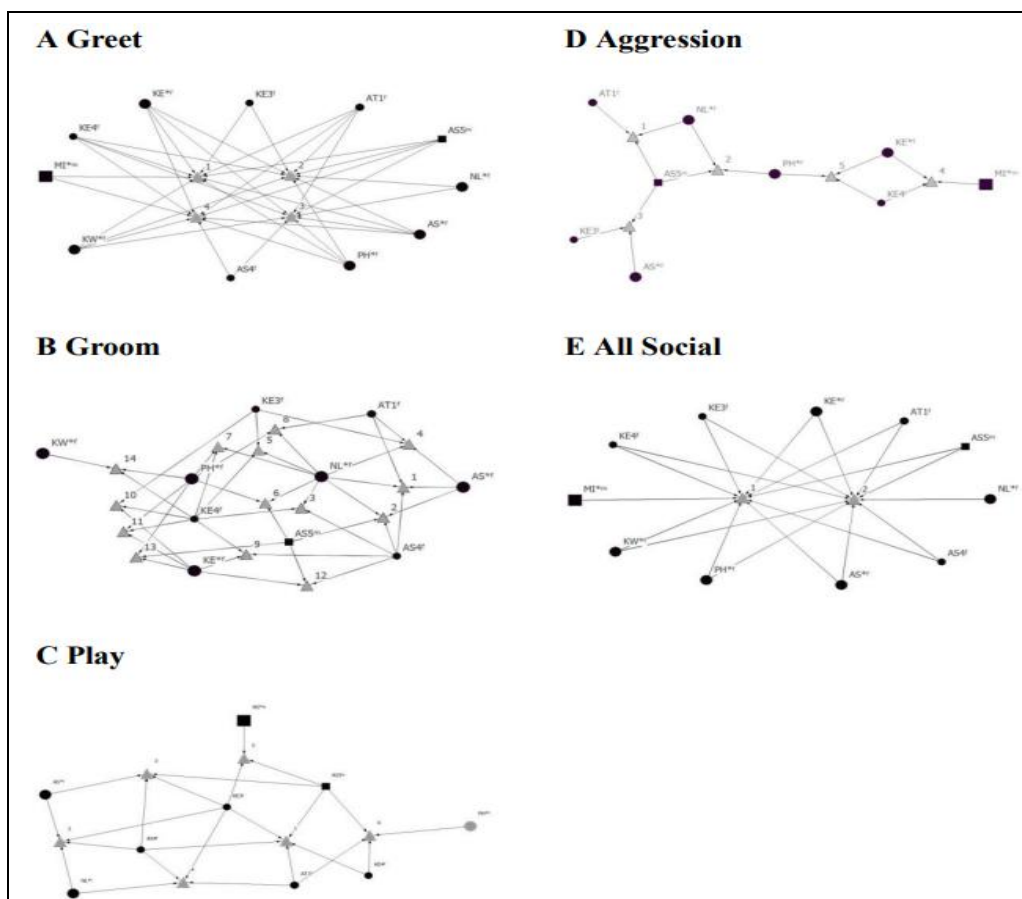
**Table 4:** Betweenness centrality values for the Ngamo pride

	Greet	Groom	Play	Aggression	All Social
AS* <sup>f</sup>	0.494	1.741	0.556	0.000	0.247
AS4 <sup>f</sup>	0.247	4.704	4.074	6.667	0.247
AS5 <sup>m</sup>	0.494	2.741	13.333	38.519	0.247
AT1 <sup>f</sup>	0.494	2.556	5.556	0.000	0.247
KE* <sup>f</sup>	0.494	2.741	0.000	29.259	0.247
KE3 <sup>f</sup>	0.247	3.593	25.185	9.259	0.247
KE4 <sup>f</sup>	0.494	9.667	21.296	0.741	0.247
KW* <sup>f</sup>	0.494	0.000	0.556	0.000	0.247
MI* <sup>m</sup>	0.247	0.000	0.000	8.889	0.000
NL* <sup>f</sup>	0.247	6.074	0.556	3.333	0.000
PH* <sup>f</sup>	0.494	10.630	4.444	18.889	0.247

\*=Captive Origin Adult; F=Females; M=Male

According to Appendix 3.1, the majority of contacts occurred among adults inside the greet, groom, and all social networks. Research indicated that adult male MI was the least inclined to initiate relationships within these

networks, unlike sub-adult or adult female NL who initiated the largest number of relationships. The Spearman's correlation confirmed this, showing a negative relationship between greet Indegree and Outdegree ( $r_s = -0.677, p = 0.022$ ).



**Fig 10:** Groups of strategic networks derived from observable social interactions.

Individuals are shown by squares and circles, while triangles denote cliques. A huge node signifies an older lion, while the form of the node indicates the sex (circles are female and squares are male).

The lions that were most often greeted as adults were also the ones that got the fewest social contacts, but they were also the ones who initiated the fewest plays. Correlation coefficients indicate a relationship of  $r_s = -0.690 (p = 0.019)$ .

for social behaviours and  $r_s = -0.767$  ( $p = 0.006$ ) for additional social behaviours.

The lionesses, who were at the center of this network, were the ones who started the most groom contacts, as shown by the A significant correlation exists between groom Betweenness centrality and groom Outdegree ( $\tau = 0.4717$ ,  $p = 0.020$ ), as shown using Kendall's tau. Appendix 3.2 demonstrates that the Mantel test revealed a positive correlation between sex and the groom network ( $r_M = 0.248$ ,  $p = 0.030$ ) suggesting the presence of a sex bias between females.

The play network was shown to be most active and linked among sub-adults. All sub-adults had higher Betweenness centrality values than adults, indicating this. The most play interactions were seen in subadults According to Appendix 3.1, male AS5 is the most likely to both initiate and receive play. Spearman's correlation revealed a positive link between aggression Indegree ( $r_s = 0.715$ ,  $p = 0.013$ ) and play Indegree, as well as between play Outdegree ( $r_s = 0.736$ ,  $p = 0.010$ ) and play Indegree. A significant correlation was identified between play Betweenness centrality and play Indegree ( $\tau = 0.610$ ,  $p = 0.003$ ), play ( $\tau = 0.602$ ,  $p = 0.003$ ), all social ( $\tau = 0.381$ ,  $p = 0.043$ ), and groom ( $\tau = 0.442$ ,  $p = 0.020$ ) Outdegree, as indicated by Kendall's tau test. All social and grooming interactions were initiated by pride members who were integral to the play network, namely the sub-adults. This indicates that they received the most engagement and also instigated the most interaction. The Mantel test (Appendix 3.2) indicates a positive correlation between the play network and both full siblings ( $r_M = 0.685$ ,  $p = 0.002$ ) and half siblings ( $r_M = 0.301$ ,  $p = 0.018$ ).

During pride feeding, 54.17 percent of the documented aggressive encounters occurred. Contested interactions among sub-adults (16.67%), adults administering punishment to sub-adults (12.5%), and the unwelcome presence of an individual among adults (16.67%) accounted for the remaining aggressive behavior. The most centrally linked KE showed discipline towards her children KE3 and KE4, as is expected of adults, especially mothers. Although KE was shown to both initiate and receive aggressive contacts, adult female PH was found to exclusively initiate such encounters, making her a less important node in the network. The members of the pride who were the most aggressive were also the ones that started the most fights, according to Spearman's correlation ( $r_s = 0.702$ ,  $p = 0.016$ ). According to Kendall's tau, the most aggressive people were located in the center of the network, and there was a positive correlation between aggressiveness Betweenness centrality and aggressiveness Outdegree ( $r_M = 0.420$ ,  $p = 0.030$ ).

### Hunting behavior

Hunting and corpse eating were studied separately in the context of hunting behavior. The prey species that the pride hunted and killed the most often was the zebra, accounting for 25% of the total. The rate of impala mortality was 18.75%, which is identical to the rate of zebra mortality. Despite guinea fowl being targeted in hunts, no birds of this species were ever killed. During the research, we watched a

single duiker hunt and fed the pride some scavenged food. The adults were seen hunting impala (23.53%) and zebra (5.88%), whereas the subadults were seen hunting duiker (4.88%), guinea fowl (17.65%).

For every hunt, four members of the pride initiated a hunting sequence, making up 4.81% of the total, and seven members of the pride joined and participated in hunting sequences, making up 4.28% of the total. There was a mean participation rate of 9.09% in the pride's carcass consuming behavior, with a range of 6.82% to 13.64%. Further analysis revealed a negative correlation ( $r_s = -0.689$ ,  $p = 0.019$ ) between aggressive network centrality and hunting behavior. There those who began hunting and had no social interactions at all had a negative tendency ( $r_s = -0.528$ ,  $p = 0.095$ ), as did those who began aggressive confrontations while hunting ( $r_s = -0.552$ ,  $p = 0.079$ ).

### Boldness test

Only adults and subadults of the female AT1 species were in the area, and they responses were captured throughout the conspecific playback. Figure 11 shows that while there was not a huge disparity in boldness test results, the boldest were the adult female AS, the least bold were the adults NL and KE, whereas the subadult AT1 was the timidest. When it came to stalking probability and degrees of aggressiveness, the adult female AS ranked first ( $r_s = 0.705$ ,  $p = 0.026$ ). The results showed a negative correlation between being bold and resting behavior ( $r = -0.494$ ,  $p = 0.074$ ). This was because KE, who was less courageous, rested more than AS and PH, who were bolder. There were positive trends in vocalizations ( $r = 0.548$ ,  $p = 0.060$ ), alert behavior ( $r = 0.494$ ,  $p = 0.074$ ), and boldness in adult females of the AS (alert alone) and KW species. Bold females are less likely to start social encounters, which may explain why there is there is a negative correlation between being bold and overall social results ( $r_s = -0.741$ ,  $p = 0.092$ ) and greet outcomes ( $r_s = -0.798$ ,  $p = 0.057$ ). It was noted that PH led the group towards the replay, but since he paused throughout the advance, he had a lower bravery score than AS.

All members of the pride were present during the hyena playback; the three most courageous females were the adults (AS, KW, and NL), whereas the three least courageous were the subadults (adult female PH, adult male MI, and AT1) (Figure 12). AS5 (a subadult male) and NL (an adult female) had significant levels of boldness, and that there was a positive correlation between boldness and M3 ( $r_s = 0.705$ ,  $p = 0.026$ ). Because courageous adult female KW engaged in a great deal of this behavior, a positive correlation between the two was noted ( $r = 0.581$ ,  $p = 0.061$ ). Bold females AS Direct movement ( $r = -0.583$ ,  $p = 0.060$ ) and aggressive Outdegree ( $r = -0.579$ ,  $p = 0.062$ ) were also lower in NL whereas less bold PH exhibited greater amounts. It was seen that adults PH and MI walked slowly towards the replay. Leading the pride throughout the progression were the sub-adult ladies, AS, and KW, with NL coming in a close second and third. The six lionesses that were evaluated for boldness in both tests did not show any significant results ( $r_s = 0.414$ ,  $N = 6$ ,  $p = 0.124$ ).

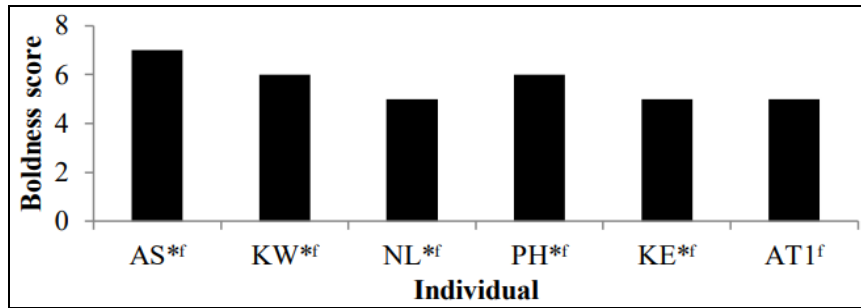


Fig 11: The bravery index of responses to lion pride video replay

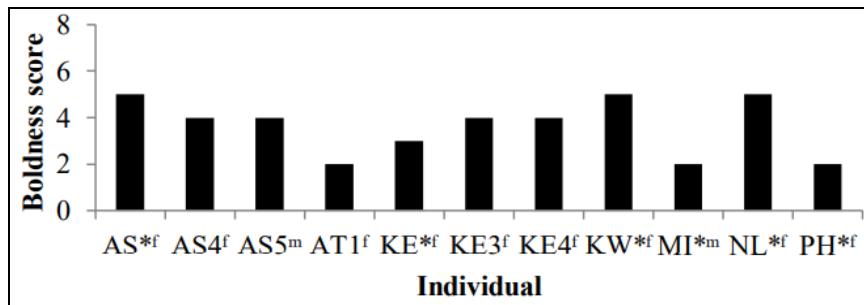


Fig 12: Levels of bravery in response to spotted hyena video

Spearman's correlation rank,  $R_s$ , and p-values for the relationships between adventurousness, activity budget, and social behaviors. The lions were ranked from 1 to 11 based on their level of boldness and proportion of engagement, which is also known as their activity budget. From most daring and likely to act to least daring and least likely to act, they were averaged to get a rating.

**Conclusion**

Lion behavior was analyzed by comparing prides born in captivity with those born in the wild, informing the evaluation of lions before ex-situ reintroduction. It was found that captive-born prides maintained wild traits, with behavior variations mainly linked to environmental factors. Successful hunting, social cohesion, and territory establishment are essential for survival post-release. The study indicated that confinement did not alter behaviors, as they were naturally expressed. The SNA suggested that identifying a social keystone could enhance future pride evaluations. Boldness testing may improve pre-release evaluations by correlating with survival rates. Overall, captive-origin lions were found to possess the necessary behaviors for self-sufficiency, emphasizing the importance of ensuring that release candidates exhibit survival behaviors in light of human-lion conflict concerns.

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