OXFORD

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An assessment of African lion *Panthera leo* sociality via social network analysis: prerelease monitoring for an *ex situ* reintroduction program

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Received on 28 October 2015; accepted on 21 January 2016

Abstract

The wild population of the African lion *Panthera leo* continues to decline, requiring alternate conservation programs to be considered. One such program is ex situ reintroduction. Prior to release, long-term monitoring and assessment of behavior is required to determine whether prides and coalitions behave naturally and are sufficiently adapted to a wild environment. Social network analysis (SNA) can be used to provide insight into how the pride as a whole and individuals within it, function. Our study was conducted upon 2 captive-origin prides who are part of an ex situ reintroduction program, and 1 wild pride of African lion. Social interactions were collected at all occurrence for each pride and categorized into greet, social grooming, play, and aggression. Betweenness centrality showed that offspring in each pride were central to the play network, whereas degree indicated that adults received (indegree) the greatest number of overall social interactions, and the adult males of each pride were least likely to initiate (outdegree) any interactions. Through the assessment of individual centrality and degree values, a social keystone adult female was identified for each pride. Social network results indicated that the 2 captive-origin prides had formed cohesive social units and possessed relationships and behaviors comparable with the wild pride for the studied behaviors. This study provided the first SNA comparison between captive-bred origin and a wild pride of lions, providing valuable information on individual and pride sociality, critical for determining the success of prides within an ex situ reintroduction program.

Key words: African lion *Panthera leo*, conservation, ex situ reintroduction, social interactions.

Introduction

The severe population decline of the African lion (*Panthera leo*) has been well documented (Bauer and Van Der Merwe 2004; Hazzah et al. 2009; Kat 2012; Riggio et al. 2013). Listed as vulnerable in Eastern and Southern Africa, and regionally endangered in Western and Northern Africa by the Bauer et al. (2015), the population of this species continues to decline despite conservation efforts.

Ex situ reintroduction is defined as the release of individuals from captive origin into the wild within the historical range of the species (New 2006). This method can be used to supplement, establish, or re-establish wild populations. Ex situ reintroduction has been successfully conducted for species worldwide (Beck et al. 1994; Sarrazin and Barbault 1996; Jule et al. 2008; Witzenberger and Hochkirch 2011), even reversing the wild extinction of California condor *Gymnogyps californianus* (Toone and Wallace 1994) and Przewalski horse *Equus caballus* (van Dierendonck and Wallis de Vries 1996; Bouman 2000). The implementation of prerelease training and assessment has resulted in increased success and postrelease survival, as demonstrated in programs for the golden lion tamarin *Leontopithecus rosalia* (Stoinski and Beck 2004), New Zealand robins *Petroica australis* (Armstrong et al. 2002), tamar wallaby *Macropus eugenii* (Griffin et al. 2001) and praire dogs *Cynomys* (Shier and Owings 2006). Ex situ reintroduction of lion prides has not yet been successfully achieved, but wild-to-wild relocations of African lions have been conducted with mixed success into Southern Africa (Hayward et al. 2006, 2007; Hunter 1998a; Hunter et al. 2007).

The mechanisms and reasons for social living of the African lion has long been of interest. The benefits and trade-offs of cooperative hunting (Stander 1992), territorial defense (Grinnell et al. 1995b), increased reproductive success and crèche rearing of young (Grinnell and McComb 1995a; Packer et al. 2001; Mosser and Packer 2009) and the effects of territory quality, pride, and population heritability and dispersal (VanderWaal et al. 2009) have been explored. Central to the success of a pride, is its social cohesion and stability. Studies that have previously investigated African lion social structure have been focused upon the egalitarianism of females (Packer et al. 2001), and describing the occurrence and frequency of interaction types for wild (Schaller 1972) and captive (Matoba et al. 2013) prides. Examining social interactions of a pride allows the influences of intrinsic and extrinsic factors upon social order to be evaluated (Crook et al. 1976), and provide indication of social dominance (Matoba et al. 2013).

Despite prides being described as stable social units, lion societies undergo fission–fusion changes, where various subgroups are constantly formed and altered, and all pride members are infrequently grouped together (Packer et al. 2001; Mosser and Packer 2009). This influences social behavior where dispersion impacts upon the opportunities for group members to participate in social behaviors (Hosey et al. 2009). The natural processes that fission–fusion societies undergo are usually inhibited in a captive environment due to limited space and small population sizes (Swaisgood and Schulte 2010). The reduction of natural dispersal and avoidance behaviors can result in increased agnostic behaviors (Morgan and Tromborg 2007), and has been found to facilitate increased social maintenance behaviors, such as greets and social grooming, in lions (Matoba et al. 2013). Whether a captive-origin impedes the development and natural expression of social behavior in African lions requires investigation. By assessing the social behavior of captive-origin prides and conducting comparisons to a wild pride, we examined whether captivity impacts the ability of a lion pride to form a cohesive unit and express social behaviors at a natural level. To achieve this, a method of critically analyzing pride sociality is required to assess a pride as a whole and at an individual level

We used social network analysis (SNA), which enables pride structure, at a group and individual level, to be quantified and assessed (Krause et al. 2007; Sih et al. 2009). Abell et al. (2013a) provided the first SNA of a captive-bred origin lion pride, determining

that the analysis was effective in assessing individuals and the pride as a whole. This study provided insight into the roles particular individuals, sexes and age groups have within a pride, which is crucial when investigating the key interactions that are present to allow social cohesion. They were also able to identify a keystone adult female within the pride. Lusseau et al. (2004) identified that individuals with high betweenness centrality values were more influential and are able to influence information flow within their group, whereas keystones have the ability to impact a group's dynamics (Sih et al. 2009). The importance of a keystone adult female within a lion pride and whether this individual is consistent within captive origin and wild prides is unknown. Whether the results found by Abell et al. (2013a) are consistent with captive-bred origin and wild prides remains unknown; an area which we endeavored to investigate to provide continued assessment of prides within an ex situ reintroduction program.

Our study was conducted upon 2 captive-origin prides managed by the African Lion and Environmental Research Trust (ALERT) situated in Zambia and Zimbabwe, and a wild pride located on the Greater Makalali Private Game Reserve (GMPGR), South Africa. In conjunction with partner organizations, ALERT manage an ex situ reintroduction conservation program for the African lion, aiming to conduct the first release of second generation prides and coalitions into the wild from captive founders (Abell et al. 2013b). Ideally, groups released will replicate those of wild prides, which consist of between 2 and 9 adult females (range of 1–18), and wild coalitions, which average between 2 and 6 adult males (range of 1–9) (Packer et al. 1991; Mosser and Packer 2009). One factor that will influence the success of this attempt is the social cohesiveness of the prides being released. Cohesiveness of groups for ex situ reintroduction is usually considered important. For wild translocations, the lack of social cohesion has been observed to increase mortality and dispersal postrelease, while locating cohesive prides and coalitions suitable for translocation is difficult (Hunter 1998b). Postrelease failure of carnivores can be due to reduced reproductive success and increased dispersal from the release site, occurrences which have been linked to a lack of group cohesion (Somers and Gusset 2009). Our study was conducted to allow interpride assessment and a comparison of social interactions between the captive origin and wild prides. Social greetings and grooming have been described as behaviors utilized to maintain social bonds between pride members in captive (Matoba et al. 2013) and wild prides, whereas play behavior is predominately conducted by cubs during their developmental stages (Schaller 1972). It is clear that each social behavior has an important role within lion pride sociality. By assessing the various types of social interactions, including greets, grooming, play, and aggression, we were able to provide insight into the importance of each, and the influence different classes of sex and age have within lion pride sociality and maintenance. We expected that this would provide insight into whether a captive-bred founder pride shows similarities and deviations in social behavior to a wild pride, while allowing an assessment of social cohesion within each pride. Such information is important to determine whether lions with captive-origin behave naturally, and are appropriate in raising offspring, which are are destined for ex situ reintroduction.

Materials and Methods

Study site and animals
The study was conducted on 2 prides of captive-bred origin, the Ngamo and Dambwa prides, and 1 wild pride, the Makhutswi pride

(Supplementary Table 1). The 2 captive-origin prides are owned and managed under ALERT, whereas the wild pride is located at the GMPGR. All prides are located within fenced reserves situated in different countries across Southern Africa.

The Ngamo pride is located 13 km outside of the township Gweru, Zimbabwe. This area consists of open grassland and dry miombo woodland, with naturally occurring species, (common duiker *Sylvicpra grimmia* and steenbok *Raphicerus campestris*) and an introduced species (impala *Aepyceros melampus*) being the prey available within the reserve at the time of the study.

The Dambwa pride is located 8 km outside of Livingstone, Zambia. The vegetation ranges from areas of grassland to woodland, with naturally occurring species (common duiker) and introduced species (impala and puku *Kobus vardonii*) being the prey available within the reserve at the time of the study.

The Makhutswi pride, the wild pride of the study, is located 50 km outside of Hoedspruit, South Africa on the GMPGR. The dominate vegetation types are mixed lowveld bushveld and mopane bushveld, with a major river system running west to east through the reserve (Druce et al. 2004). Many large mammals are located on the reserve, including hippopotumus *Hippopotamus amphibius*, elephant *Loxodonta*, giraffe *Giraffa camelopardalis*, various species of antelope (duiker, steenbok, impala, kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus sylvaticus* and nyala *Tragelaphus angasii*), warthog *Phacochoerus*, zebra *Equus burchellii*, wildebeest *Connochaetes* and various species of large predators (spotted hyena *Crocuta crocuta*, brown hyena *Hyaena brunnea*, cheetah *Acinonyx jubatus* and leopard *Panthera pardus pardus*). The reserve has a large lion population, with 3 prides (including the study pride), 2 bachelor groups and a nomadic female with 2 cubs, combined to an estimated total of 34 individuals at the time of the study. This population originates from wild translocations of lions released into the reserve from other reserves across Southern Africa, with the first release occuring in December 1994 (Druce et al. 2004).

Data collection

The same observational methods were applied to all prides, where the time of day observations were collected being the only variation in data collection between prides. Social interaction and pride composition data was collected via direct observations from a research vehicle. Observations were conducted upon each pride between 0630 h and 1700 h for the Dambwa pride, 0630 h and 1830 h for the Ngamo pride, and 0630 h and 1930 h for the Makhutswi pride. Observations were a minimum of 1 h to a maximum of 3 h each, and conducted up to 3 times a day.

We recorded pride compositions at the beginning and end of each observation session, or after a change in composition occurred (either a pride member leaves or joins the observed group) with each individual being recorded as present or absent.

We used all occurrence sampling when recording social interactions, with interaction type, individual who initiated and received the interaction, and whether it was accepted, ignored, or rejected recorded. A social interaction bout was deemed to have ceased once the interaction was not observed for more than 1 min. If during an encounter, more than 1 type of social interaction was observed, the initial interaction type was recorded only, avoiding pseudoreplication. The total number of interactions collected for each pride was calculated for each social interaction category; greet, social grooming, play, and aggression, described previously by Schaller (1972).

Statistical analysis

Social interaction data were standardized for each pride on a pairwise and hour basis. In total, the prides were observed on 46, 20, and 26 separate occassions for the Ngamo, Dambwa, and Makhutswi prides, respectively. During these observations, the Ngamo pride was observed for 98 hr, where a total of 667 interactions were recorded. The Dambwa pride was observed for 67 hr where 841 interactions were recorded. The Makhutswi pride was observed for 62 hr, where 162 interactions were recorded. Social interaction data were compiled into assymetrical (directional), weighted matrices for greet, social grooming, play, aggression, and all social interaction types. Social interactions for each matrix were standardized by dividing the number of interactions collected per pair of lions by the total number of hours each pair was observed together, per pride. Pride composition was compiled into a symmetrical matrix, prior to using a modified ratio index detailed in Abell et al. (2013a) to generate individual association within the pride.

Social interactions were analyzed at an individual (degree and betweenness centrality) and pride level (density and clique) for each of the 3 prides.

All matrices were analyzed via SNA statistical program UCINET, version 6.543 (Borgatti et al. 2002). We calculated density, degree (indegree and outdegree), betweenness centrality, and clique groups for each network per pride. Density is the proportion of all possible connections within a matrix, with a high value (1) representing a highly connected network, and a low value (0), an unconnected network (Wasserman and Faust 1994; Wey et al. 2008). Degree shows the number of direct connections an individual has with other network members (Wasserman and Faust 1994). As the social interaction matrices were directional, degree describes the number of interactions received (indegree) and initiated (outdegree) for each individual (Wey et al. 2008; Sih et al. 2009). Symmetrical matrices were generated prior to calculating betweenness centrality and cliques for each network per pride. Betweenness centrality indicates the involvement of an individual within a network, evaluating the number of shortest paths which are required to pass before reaching a target individual. A higher value indicates a more central member, as this individual connects others within the network who may not be directly connected, serving as a bridge between and connecting subgroups (Krause et al. 2007; Croft et al. 2008; Wey et al. 2008). UCINET generated normalized indegree and outdegree values that were tested for dependence within and between networks for each pride via a Spearman's correlation in Genstat 17th Edition (VSN International 2014). Kendall's tau correlations were conducted upon normalized degree and betweenness to assess whether associations between social influence and social power existed within each pride (Abell et al. 2013a).

We used NETDRAW, version 2.1476 (Borgatti et al. 2002) to generate sociograms and clique figures for social interaction networks. Matrices were directional: thus line thickness illustrates the strength of association between nodes (lions), where a thicker line indicates a stronger association (Croft et al. 2008), whereas arrows indicate the direction of interaction between nodes (Wey et al. 2008). SOCPROG version 2.4 (Whitehead 2009) was used to conduct a Mantel test, which allowed us to assess for similarities between social interaction matrices and age, gender, kinship, pride composition, and a random network. The random network within this analysis was generated in UCINET for each pride (Abell et al. 2013a).

Results

Analyses showed that adults and offspring within each pride have roles that differ between networks, indicated by degree and betweenness centrality. All interaction networks were found to not significantly associated with a random network, indicating interactions were nonrandomly distributed within each pride. Cubs and subadults were likely to be initiators of the most all social and greet interactions, while being central to the play network. Adult males across the 3 prides were found to receive high levels of all social interactions, while being least likely to initiate any type of interaction. By viewing and comparing degree, betweennness, and clique involvement between adult females within a pride, a keystone individual was able to be identified. Density values for the all social and greet matrices for the Ngamo and Dambwa prides, and to a lesser extent the Makhutswi pride, indicate that each of the prides are highly connected (Table 1). For the remaining matrices, density values were low, indicating that not all individuals where involved or fully connected within the network. Overall, the Makhutswi pride was observed to have a lower density value for each social interaction networks compared to the Ngamo and Dambwa pride (Table 1).

The all social (Figure 1) and greet (Figure 2) matrices for each of the 3 prides indicate that the majority of pride members are connected. For the Ngamo pride, interactions between the pride male

MI and adult female NL were nonexistent in A1 and D1, whereas for the Makhutswi pride, adult female MID was absent in the greet matrix and along with adult male MA, is not highly connected. These observations were reflected in the clique (Figure 2) and centrality (Figure 3) analysis for the greet network. Four cliques were observed for the Ngamo pride (A1), with subadults AT1 and AS5, and adults MI and NL involved in 2 cliques each. These 4 pride members were also found to have the lowest centrality value for this network. The Makhutswi pride had 5 cliques, with adults MA and MID being absent in all cliques, whereas adult female DE was present in 1 clique, which is reflected in the centrality value (Figure 3) for these 3 lions.

Clique figures for all social matrices show the least connected individuals per pride (Figure 1). Both the Dambwa and Makhutswi prides had members absent in the clique analysis; subadult RS3 was absent from the observed clique, while along with RS2, had low centrality. Three cliques were observed for the Makhutswi pride, with adults MA and MID absent in all, and along with DE, had low centrality. Absence from a clique network indicates that an individual lacks significant connections with clique members (Wasserman and Faust 1994; Wey et al. 2008).

The groom matrices (Figure 4) showed that for the Ngamo pride, the strongest ties were observed to occur between cubs and their mothers, an occurrence observed to a lesser extent in the Dambwa pride. For the Makhutswi pride, adult males MA and XI, and adult female MID, were absent from the network, with the strongest tie lied between half-sibling males SA and LI.

The most centrally connected individual for each pride in the play matrix was a male subadult (AS5 for Ngamo) or a male cub (LE1 for Dambwa and LI for Makhutswi) (Figure 3). For both the Ngamo and Makhutswi prides, all of the adults had low centrality, indicating they were not points of connection within this network. Interestingly, 3 of the 6 adults (KE, KW, and LE) in the Dambwa pride were also not points of connection, with the remaining adults
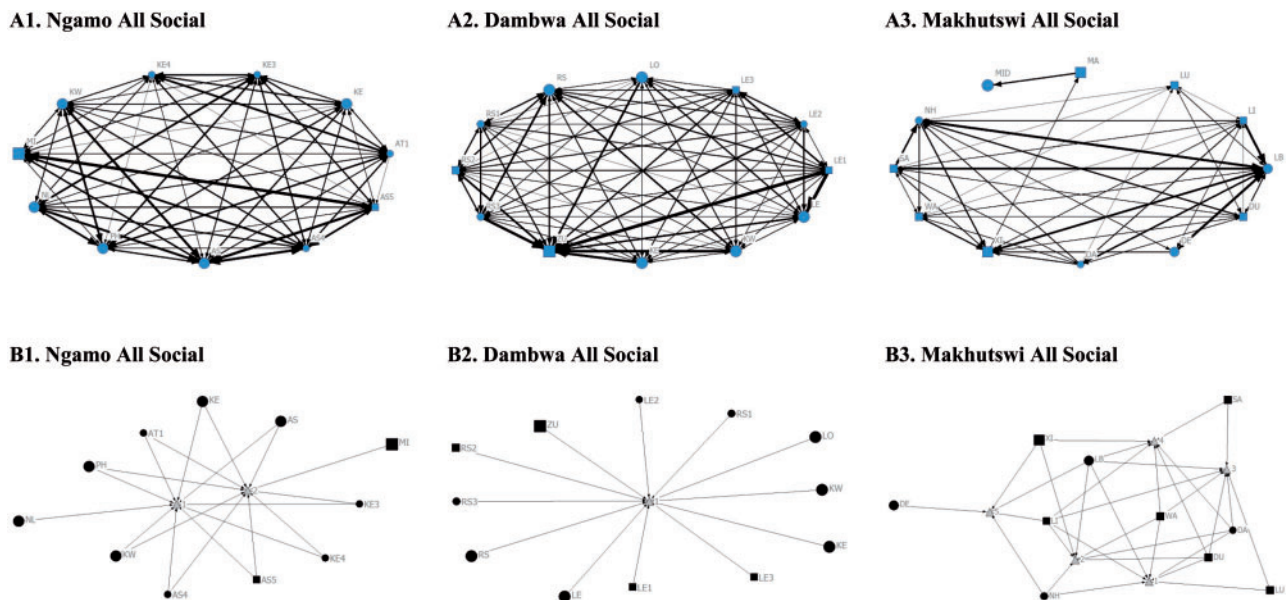
Table 1. Density values for each network per pride, with a range of 0 (unconnected) to 1 (highly connected)

| Pride	Greet	Groom	Play	Aggression	All social	Pride composition
Ngamo	0.891	0.664	0.145	0.136	0.964	1
Dambwa	0.780	0.303	0.515	0.068	0.939	1
Makhutswi	0.394	0.091	0.114	0.053	0.492	1

Figure 1. Sociogram and clique matrices calculated from observation of all social behaviors. (A1–A3) are the sociograms, whereas (B1–B3) are the calculated clique matrices for the groom network for each pride. For the sociograms and cliques, squares and circles are nodes, representing an individual, whereas for the cliques, triangles signify a clique. Node shape represents the sex of a lion (circles are female, squares are male), whereas the node size is directly proportional to the age of the individual (larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of association between individuals.

having reduced involvement (compared to the cubs) (Figure 5). It could have been expected that adult female LE would have higher play centrality due to being the mother of LE1, LE2, and LE3, as observed for adult female RS. It is clear for all prides that offspring were central to the play network.

Low levels of aggression were observed for each pride, with sub-adult males being the most centrally connected (Figure 3) for the Ngamo (AS5) and Makhutswi (SA) prides. Interestingly, adult female LE for the Dambwa pride was the most centrally connected individual for the aggression network, despite us observing no
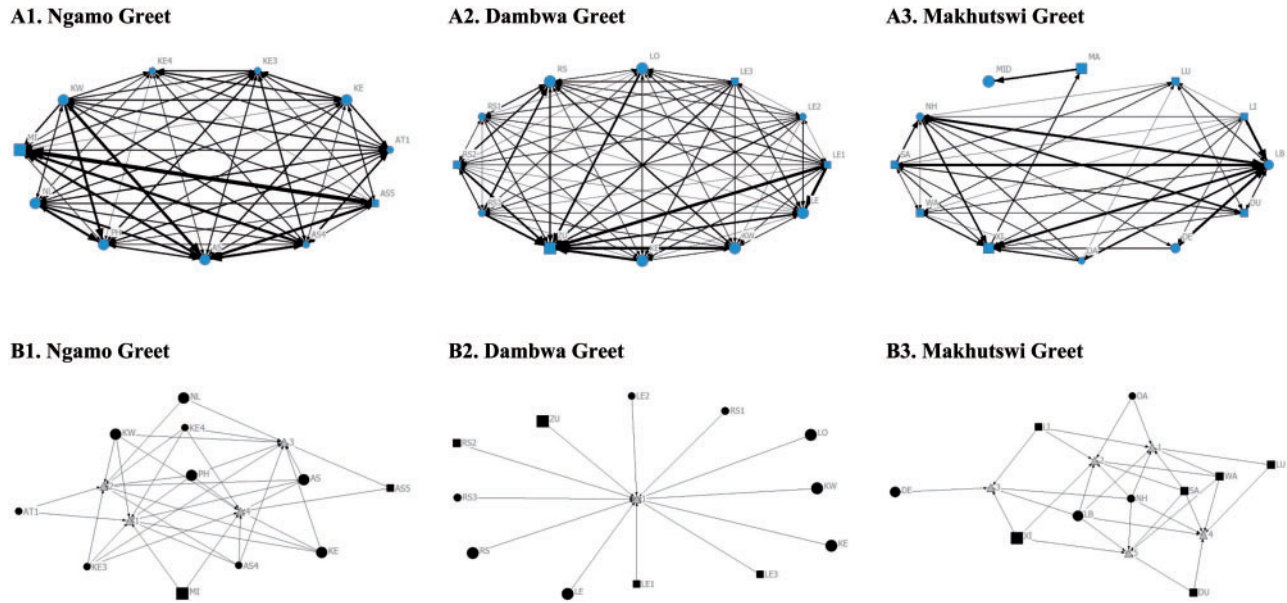
Figure 2. Sociogram and clique matrices calculated from observation of greet behaviors. (A1–A3) are the sociograms, whereas (B1–B3) are the calculated clique matrices for the greet network for each pride. For the sociograms and cliques, squares and circles are nodes, representing an individual, whereas for the cliques, triangles signify a clique. Node shape represents the sex of a lion (circles are female, squares are male), whereas the node size is directly proportional to the age of the individual (larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of association between individuals.
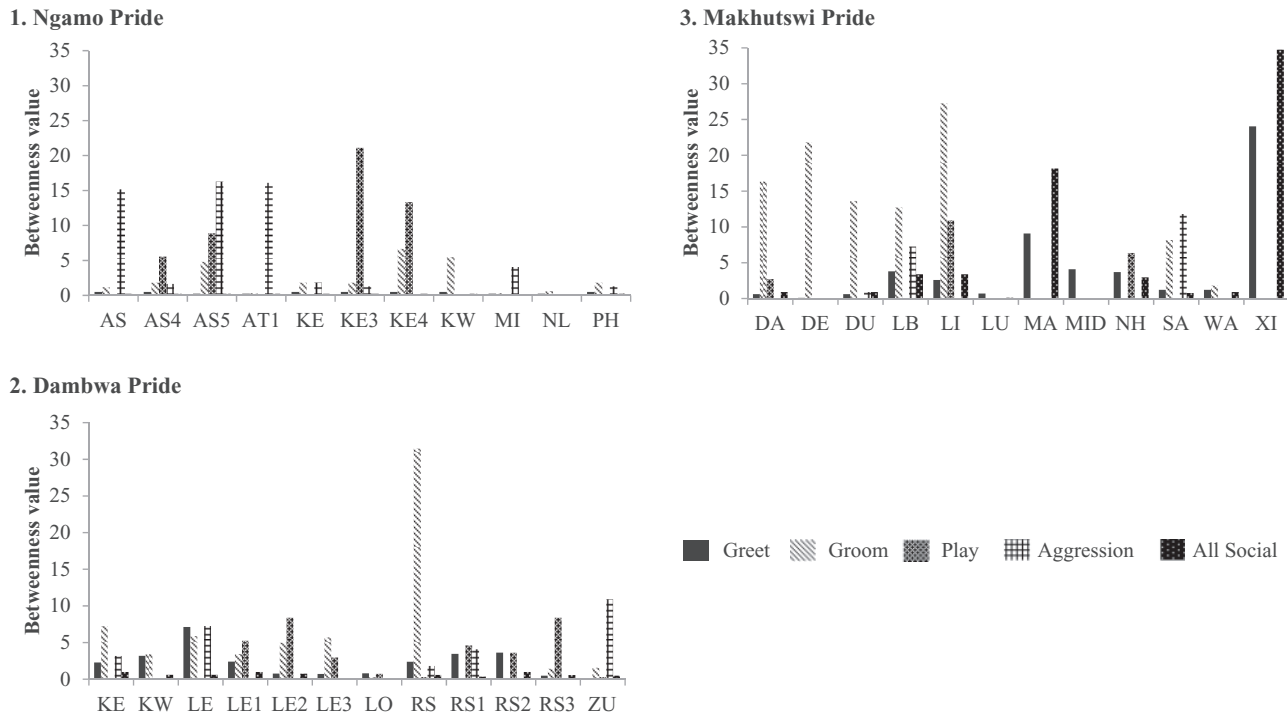
Figure 3. Betweenness centrality for each network. Calculated normalized betweenness centrality for the greet, groom, play, aggression, and all social networks, per individual for each pride.
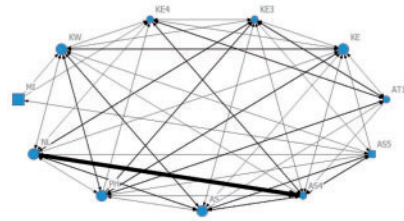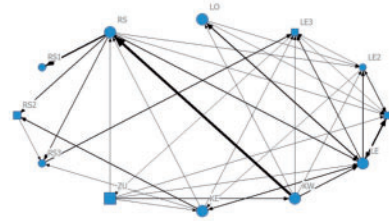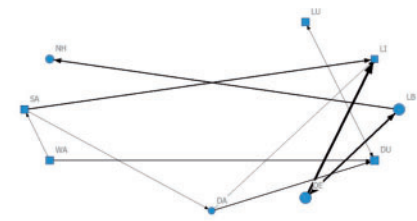
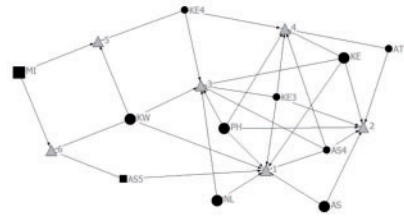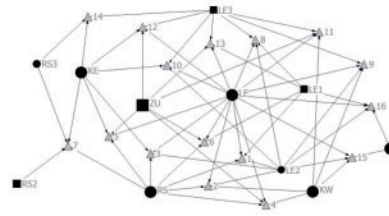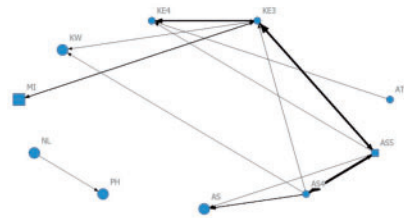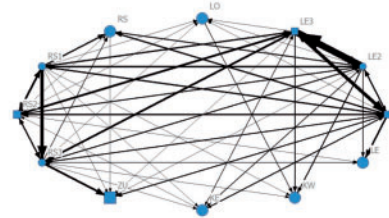**Figure 4.** Sociogram and clique matrices calculated from observation of groom behaviors. (A1–A3) are the sociograms, whereas (B1–B3) are the calculated clique matrices for the groom network for each pride. For the sociograms and cliques, squares and circles are nodes, whereas for the cliques, triangles signify a clique. Node shape represents the sex of a lion (circles are female, squares are male), whereas the node size is directly proportional to the age of the individual (larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of association between individuals.
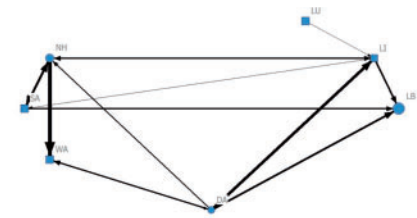

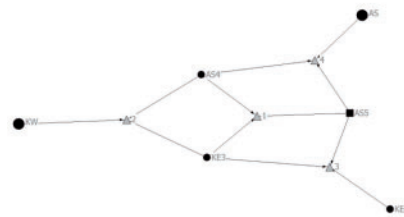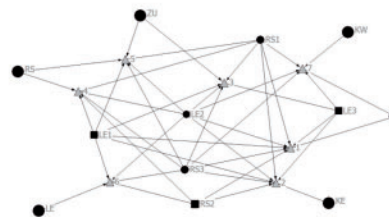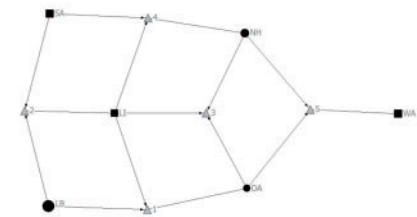**Figure 5.** Sociogram and clique matrices calculated from observation of play behaviors. (A1–A3) are sociograms, whereas (B1–B3) are the calculated clique matrices for the play network, for each pride. For the sociograms and cliques, squares and circles are nodes, whereas for the cliques, triangles signify a clique. Node shape represents the sex of a lion (circles are female, squares are male), whereas the node size is directly proportional to the age of the individual (larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of association between individuals.

aggression between LE and her cubs, resulting in the cubs being absent from the network. A connection between a lioness and 1 of her offspring was observed for the Dambwa (RS and RS1), and Ngamo pride (AS and AS4). No other connections between mothers and their offspring were observed in the aggression network (Figure 6).

Interactions received (indegree) and initiated (outdegree) per individual for each pride indicated the role an individual plays within an interaction (Figures 7 and 8). For all 3 prides, an adult pride member was observed to receive the greatest (Ngamo = AS, Dambwa = ZU, and Makhutswi = LB), and initiate the lowest (Ngamo = MI, Dambwa = ZU, and Makhutswi = MID) number of overall social interactions, whereas a subadult or cub was most likely to initiate the most social interactions (Ngamo = AS5, Dambwa = LE1, and Makhutswi = SA) (Figure 8). Spearman's correlation found all social indegree and outdegree for the Dambwa and Makhutswi prides to be negatively correlated ($\tau = -0.727$,
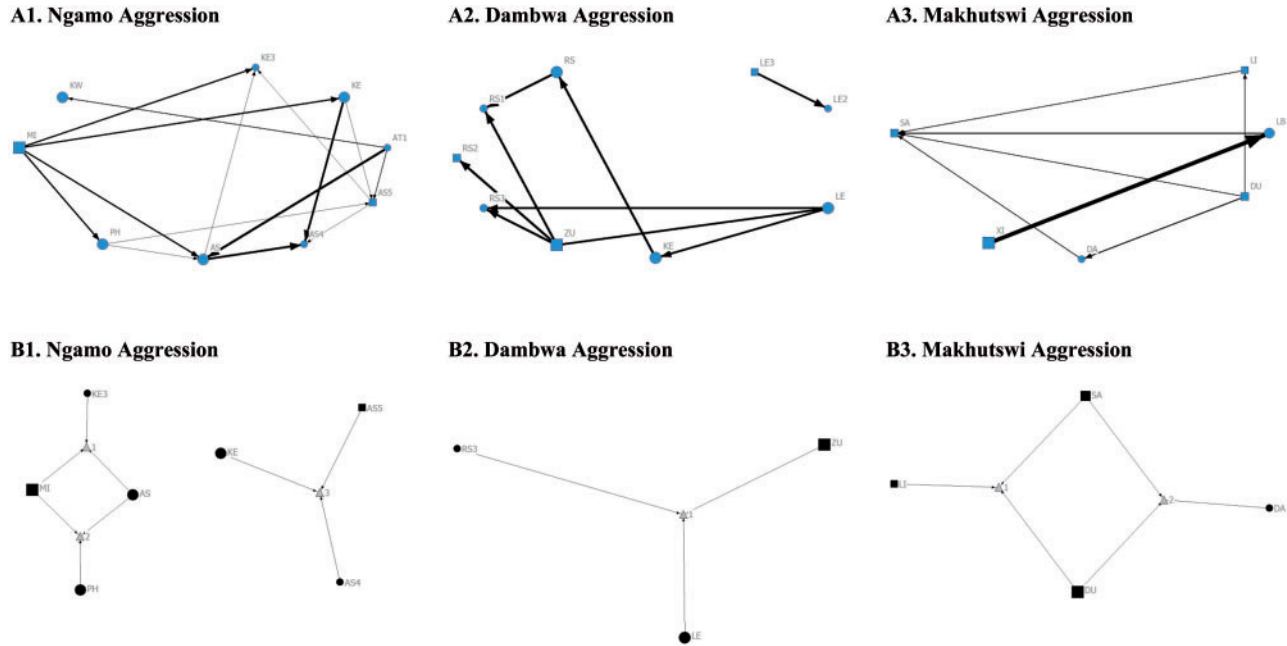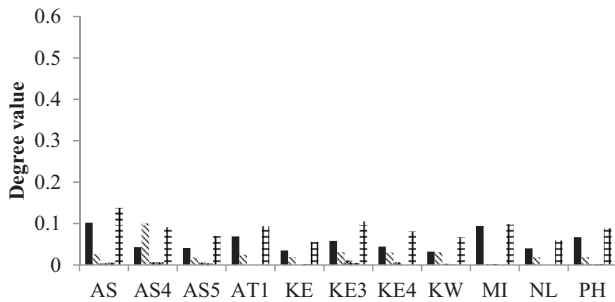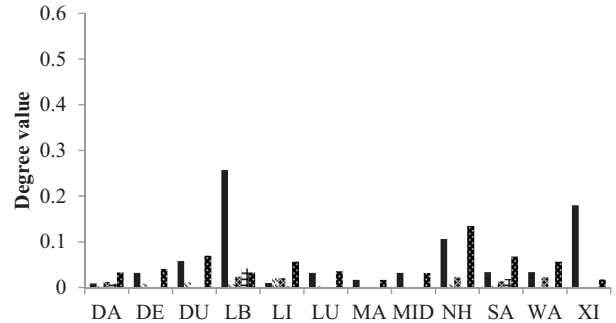
Figure 6. Sociogram and clique matrices calculated from observation of aggression behaviors. (A1–A3) are sociograms, whereas (B1–B3) are the calculated cliques for the aggression network, per pride. For the sociograms and cliques, squares and circles are nodes, whereas for the cliques, triangles signify a clique. Node shape represents the sex of a lion (circles are female, squares are male), whereas the node size is directly proportional to the age of the individual (larger the symbol, the older the lion). For the sociograms, line thickness between dyads represents the strength of association between individuals.
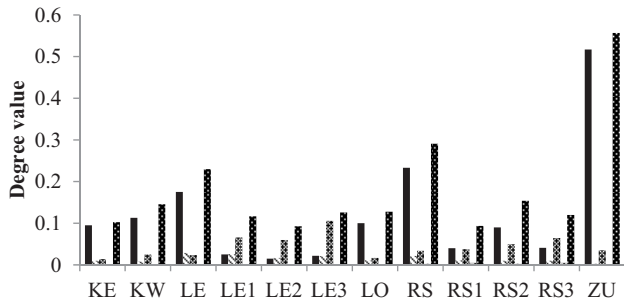

Figure 7. Indegree for each network. Calculated normalized indegree for the greet, groom, play, aggression, and all social networks, per individual for each pride.

$P = 0.007$; $\tau = 0.729$, $P = 0.002$). For the Dambwa pride, those who received the most all social interactions (Figure 7) received the most greetings ($\tau = 0.832$, $P = 0.001$) and initiated the fewest greetings ($\tau = -0.623$, $P = 0.030$), social grooming ($\tau = -0.820$, $P = 0.001$) and play encounters ($\tau = -0.820$, $P = 0.001$). Pride members who

initiated the most all social interactions were also found to initiate the most greetings ($\tau = 0.876$, $P = 0.000$), social grooming ($\tau = 0.785$, $P = 0.003$) and play encounters ($\tau = 0.785$, $P = 0.003$). For the Makhutswi pride, those who received the most cumulative social interactions initiated the most greets ($\tau = 0.767$, $P = 0.001$)

A1. Ngamo Pride

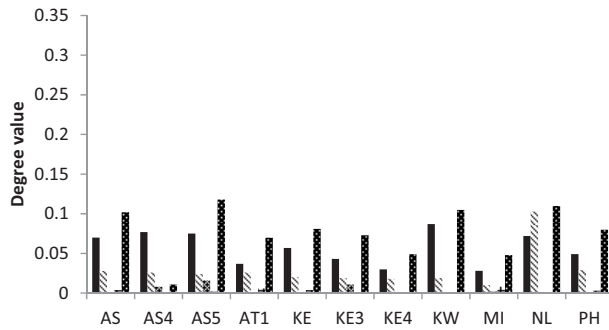**A2. Dambwa Pride**

A3. Makhutswi Pride

■ Greet ▨ Groom ▧ Play ▦ Aggression ▨ All Social

Figure 8. Outdegree for each network. Calculated normalized outdegree for the greet, groom, play, aggression, and all social networks, per individual for each pride.
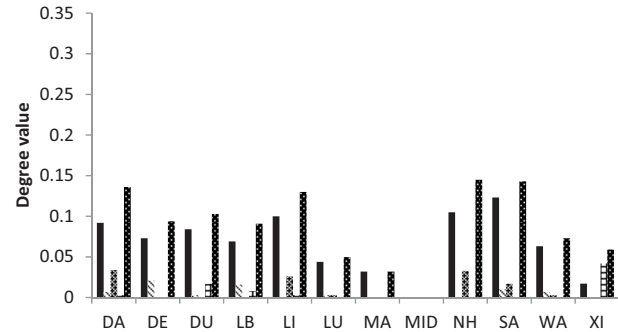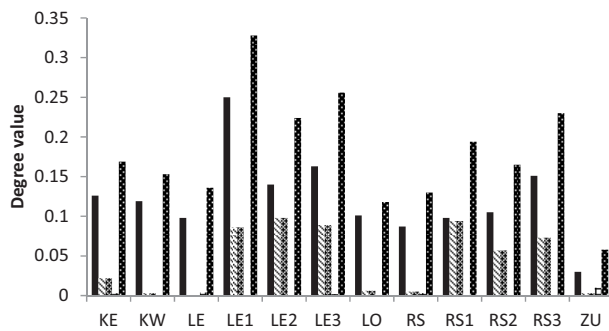
and play encounters ($\tau = 0.436$, $P = 0.039$). The Mantel tests per pride found a positive association between social interactions and full siblings ($_rM = 0.133$, $P = 0.039$, and $_rM = 0.403$, $P < 0.001$) and age ($_rM = 0.145$, $P = 0.022$ and $_rM = 0.403$, $P < 0.001$), respectively, for the Dambwa (Supplementary Table 3) and Makhutswi (Supplementary Table 4) prides.

Greet indegree and outdegree was found to be negatively associated for the Ngamo ($\tau = -0.627$, $P = 0.039$) and Dambwa ($\tau = -0.785$, $P = 0.003$) prides. For the Dambwa pride, lions who received the most greetings (adults) initiated the fewest cumulative social ($\tau = -0.888$, $P = 0.000$), social groom ($\tau = -0.935$, $P = 0.000$) and play encounters ($\tau = -0.935$, $P = 0.000$), and initiated the most aggression ($\tau = 0.610$, $P = 0.035$). The Mantel test for the greet network for the Makhutswi pride was found to be positively associated with full siblings ($_rM = 0.188$, $P = 0.015$) and age ($_rM = 0.188$, $P = 0.019$).

Offspring were observed to receive the greatest number of groom interactions; AS4 for the Ngamo and DA for the Makhutswi prides (Figure 7). Adult female LE was observed to receive and initiate the highest number of grooming interactions for the Dambwa pride. Pride males in each pride all received the fewest number of grooming interactions, and for the Ngamo and Makhutswi pride, were also least likely to initiate this interaction type. For the Makhutswi pride, the test of association found groom centrality to be positively associated with groom indegree ($\tau = 0.637$, $P = 0.008$), and greet outdegree ($\tau = 0.493$, $P = 0.032$), indicating the lions who were central to the groom network received the most groom and initiated the most greet interactions. The Mantel test for the groom network found a positive association with sex ($_rM = 0.170$, $P < 0.001$; $_rM = 0.217$,

$P = 0.018$) for the Ngamo and Makhutswi prides, respectively. A positive association between the groom network and full siblings ($_rM = 0.250$, $P = 0.027$) and age ($_rM = 0.250$, $P = 0.029$) was also found for the Makhutswi pride.

Cubs and subadults, in all prides, were observed to initiate and receive the greatest number of play interactions (Figures 7 and 8). This is expected as related offspring of similar age are central to play networks. Spearman's correlation found play indegree and outdegree to be positively associated for the Dambwa ($\tau = 0.680$, $P = 0.015$) and Makhutswi ($\tau = 0.764$, $P = 0.004$) prides. For the Dambwa pride, individuals who received the most play interactions also initiated the most social ($\tau = 0.741$, $P = 0.006$), greets ($\tau = 0.581$, $P = 0.047$) and social grooming encounters ($\tau = 0.680$, $P = 0.015$). The individuals (cubs and subadults) who received the most play interactions also initiated the greatest social ($\tau = 0.656$, $P = 0.021$) and greet ($\tau = 0.604$, $P = 0.038$) interactions. Kendall's tau analysis for each pride found prides to have a positive association between play centrality and play indegree (Ngamo [$\tau = 0.744$, $P = 0.004$] and Dambwa [$\tau = 0.583$, $P = 0.010$]) and play outdegree (Ngamo [$\tau = 0.607$, $P = 0.024$], Dambwa [$\tau = 0.667$, $P = 0.003$] and Makhutswi [$\tau = 0.620$, $P = 0.019$]). In addition, the Dambwa pride was found to have a positive association between play centrality and groom outdegree ($\tau = 0.667$, $P = 0.003$) and a negative association with aggression outdegree ($\tau = -0.540$, $P = 0.029$) and greet indegree ($\tau = -0.552$, $P = 0.015$). The Makhutswi pride was also observed to have additional positive associations between play centrality and social ($\tau = 0.494$, $P = 0.045$) and greet ($\tau = 0.494$, $P = 0.045$) outdegree matrices. This shows that cubs and subadults of this pride initiated the most greet and overall social interactions.

In all prides, there was a positive association between their play matrices and half siblings (Ngamo [$_rM = 0.300$, $P = 0.018$], Dambwa [$_rM = 0.386$, $P < 0.001$] and Makhutswi [$_rM = 0.333$, $P = 0.014$]). A positive association between the play matrices and full siblings for both the Ngamo ($_rM = 0.445$, $P = 0.003$) and Dambwa ($_rM = 0.508$, $P = 0.001$) prides and age for the Dambwa pride ($_rM = 0.286$, $P = 0.002$) were also found.

Discussion

The comparison of 2 captive-origin prides with a wild pride permitted us to identify similarities and differences in social behavior, at an individual and pride level. Networks across the 3 prides were found to be nonrandom, demonstrating that individuals exhibit a choice in associating with other pride members. Consistent similarities were found between all prides. Cubs and subadults were persistently found to have integral roles in the play network, whereas adults were observed to receive the most and initiate the least greet and overall social interactions. Differences between prides were observed to occur at an individual level, where the involvement of a particular individual, sex or age group differed slightly between the prides.

Density of the Makhutswi pride was less than the 2 captive-bred origin prides, possibly due to the lack of involvement of 2 pride members, which were often dispersed from the observed group. Schaller (1972) observed that a wild pride is not socially cohesive in terms of all pride members are consistently together, but because lions live in a fission–fusion society, it is more likely members and groups can often be dispersed (Packer et al. 2001; Mosser and Packer 2009). We need to be mindful of this when comparing between captive origin and wild prides where, for ex situ reintroduction, social cohesion is thought to be essential for postrelease success. Therefore, the evaluation of social cohesiveness of a group prerelease is important, and assists in identifying prides and coalitions that are suitable for release. The high cohesion of the 2 captive-bred origin prides indicates that it is possible to construct a cohesive pride from captive founders, and result in a socially connected unit that appears well suited to release in terms of cohesiveness.

Overall, fewer interactions were observed for the Makhutswi pride compared to the captive-bred origin prides. Factors that may have resulted in a reduced social interaction frequency vary, including pride dispersal, territory size, and rearing history. Adult presence for the Makhutswi pride, the wild pride, was low compared to the captive-bred origin prides. Male absence was suspected to be a result of time spent with another pride within their territory and conducting territorial behaviors. Absence is a natural occurrence, where male dispersal from the pride can average 12 and range up to 15 months (Funston, et al. 2003; Matoba et al. 2013), while Schaller (1972) has described adult males to be "transitory pride members." Adult female MID was an older pride member (14 years old) and had sustained an injury which prevented this lioness from keeping up with pride movements, and instead was observed briefly with daughter DE on 2 occasions. The elevated interactions and male presence we observed for the captive-origin prides could be accounted for by the differences in reserve sizes. Restricted territories impede upon a pride's ability to undergo fission–fusion changes, resulting in more members of the pride being located toegther more frequently. The Ngamo and Dambwa prides were located in reserves smaller than the Makhutswi pride (Supplementary Table 1). Captive animals are not required to spend time performing some behaviors, such as foraging, which can result in more time spent conducting

social behaviors (Matoba et al. 2013). Although territorial sizes are impacted upon by various factors, including prey availability and pride size, the fenced reserves of the captive-origin prides do not equate to the estimated territories sizes of wild prides; range of 120–400 km^2 (Schaller 1972), and mean of 56 km^2 (range of 15–219 km^2) (Mosser and Packer 2009) for prides within the Serengeti, and 52.4 ± 26.3 km^2 for 5 prides in the Selous Game Reserve, Tanzania (Spong 2002). The captive history of the Ngamo and Dambwa adult males must also be considered. Ngamo male MI was not raised or housed with any of the pride adult females prior to release into the reserve, whereas Dambwa male ZU was. This difference in history could account for ZU's consistent presence with the pride, due to the familiarity with the pride females. Naturally, males disperse from their natal pride by the age of 4 years (Pusey and Packer 1987), live a nomadic life or form coalitions and compete for succession of a pride (Schaller 1972; Packer et al. 1991). These variations suggest that individual history and the surrounding environment impact upon behavior, however, the extent is unknown. Whether male behavior of the captive-bred origin prides would change if released into larger reserves is yet to be determined.

Adults, subadults, and cubs were found to have different roles within pride sociality. Across all prides, the highest receiver was an adult, whereas offspring were more likely to initiate all social interactions. Schaller (1972) also observed this pattern for wild prides, with cub-to-adult female interactions accounting for 62%, and adult female-to-cub 11% of all observed interactions. Similarity between captive-bred origin and wild prides suggests that a captive history has not impacted upon this behavior. Cubs and subadults of the 3 prides were central to the play network. For the Dambwa and Makhutswi prides, play was the second most observed interaction type (after greets), which could be attributed to the cubs (< 2 years). Although older pride members do take part in play behavior, our results confirm those of Schaller (1972) who reported that cubs play at a higher frequency, duration, and intensity compared to subadults and adults.

Adult males across the 3 prides were receivers of social encounters, however, rarely initiated social interactions. A sex bias was observed in the Ngamo pride for greet and groom interactions, with lionesses directing these interactions to other females. These findings indicate that sex may impact the distribution of social interactions within a pride. Schaller (1972) also observed that wild males rarely initiated greets or grooming with other pride members and described greets as peaceful interactions between pride members, symbolizing acceptance and belonging to a pride. This possibly accounts for the elevated number of interactions pride males receive, opposed to the number they initiate. Sex prefence has been observed in zoological captive lions, with Matoba et al. (2013) observing that males greeted other males and females groomed other females at high frequencies. Male to male interaction bias was difficult to properly evaluate because the Makhutswi pride was the only 1 with a coalition. The adult males of this pride were infrequently observed together, or with the pride, which could be attributed to various factors. Within the established territory, this male coalition held tenure over 2 prides, requiring time to be split between these prides and territorial patrolling. Additionally, the vegetation type(s) within a territory can also influence male behavior. The Makhutswi territory was covered in open and closed woodland. Funston et al. (1998) observed that males were more frequently present with their pride in open plain, compared to woodland habitat. Dense vegetation impacts visibility, requiring additional movement to explore all areas.

The extent to which the Makhutswi males are absent from the 2 prides requires further investigation.

A keystone adult female was identified in each of the 3 prides; PH, RS, and LB for the Ngamo, Dambwa, and Makhutswi prides, respectively. These keystone females were identified by comparing degree values, involvement within cliques and betweenness centrality values across all of the social matrices. At the time of our study, 2 of the 3 females had mothered cubs within their prides (RS and LB) and were all of similar age (7–9 years old). These females were integral to the majority of networks, and connected peripheral members to the rest of the pride. The presence of a keystone female in the Makhutswi pride suggests that this role is an integral component of a wild pride, while indicating that a captive history does not impact upon a females' ability to establish and fulfill this role.

SNA provides us with the ability to identify a keystone female and further studies should focus on identifying the extent to which this role is essential to pride cohesion. Whether the removal of a keystone female would result in the dissociation of a pride, or whether the role would be filled by another female, is unclear. Lusseau et al. (2004) found within bottlenose dolphin *Tursiops truncates* societies that a keystone individual is required in maintaining group cohesion, whereas Flack et al. (2005) determined that such individuals are important in minimizing conflicts and facilitate positive interactions between group members. Postremoval of a keystone individual can result in a reduction of positive and an increase in agnostic interactions, which results in a conservative and less incorporated society (Flack et al. 2006). This indicates that a lion pride could experience pride dispersion and fragmentation postremoval of a keystone adult female. However, we suggest that the changes a pride would experience may not be universal. The impact may differ according to the composition and environment of the pride at the time. If a pride consists of peripheral members, this pride could be more likely to fragment, whereas a highly connected pride, or one that contains cubs, may be more likely to remain cohesive. Lastly, the Ngamo prides' keystone female was PH whom has been previously recognized by Abell et al. (2013a) as a keystone female. These 2 studies indicate that the position of this role is relatively stable over a period of time. Additional studies should consider these influences and investigate the degree to which keystone females are critical to pride cohesion.

On the whole, we obtained valuable information on pride and individual sociality by conducting SNA and comparisons between captive origin and a wild pride. The role a keystone female plays within a pride is important though it is unclear whether this is so in all prides and environments. Similarities that were observed between the 3 prides, and published between wild and zoological prides, indicate many aspects of social behavior are stable, and resilient to the captive environment. This suggests that captivity does not impede upon the ability of a pride to become socially cohesive, nor an individual being able to express normal social behavior if prerelease training, and environmental conditions facilitate adaptive natural behaviors and experiences. This information is vital in the continued monitoring and assessment of prides within an ex situ reintroduction program. The next step requires the assessment of prides and coalitions post ex situ reintroduction.

Funding

Acknowledgments

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