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Exploring African lion (*Panthera leo*) behavioural phenotypes: individual differences and correlations between sociality, boldness and behaviour.

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ABSTRACT

Increasing our understanding of personality, at an individual and group level, is crucial to the pre-release assessment of social species within ex-situ reintroduction programs. We conducted the first exploration into personality of a captive-origin pride of African lions (*Panthera leo*), assessing behavioural variations and consistencies in daily activity, social and hunting behaviour, and boldness. Data were collected via direct observations, while a species specific protocol for testing boldness, using playbacks, was developed. Differences in sex, age and session time for the activity budget were evaluated using Pearson correlations and repeated measures ANOVA, while social interactions were analysed using Social Network Analysis (SNA). Spearman's correlations were conducted to assess for associations between boldness scores, activity and sociality. The two boldness tests provided a range of scores per lion, indicating the test was effective. Correlations and variations in individual behaviour indicated that adults and sub-adults have specific roles within pride behaviour. Correlations between boldness, and activity and social behaviours provided information upon the role of individuals, allowing investigation into the behaviour of dominant and a social keystone. Our study indicates that evaluating various aspects of behaviour in conjunction with boldness has the potential to assist the pre-release assessment of a pride within an ex-situ reintroduction program.

Introduction

The African lion (*Panthera leo*) has suffered large population declines, with estimates in the 1950s, 500,000 (Hazzah et al. 2009), dropping to between 23,000 (Bauer and Van Der Merwe 2004) and 32,000 (Riggio et al. 2013) today. Deduced from analysing 47 subpopulations, the IUCN states that lion populations have suffered an approximate 43% decline over the past 21 years (Bauer et al. 2015). Despite in-situ conservation efforts, populations continue to decline, requiring other methods to be explored (Abell et al. 2013a; Abell et al. 2013b). Lion reintroductions from wild sources have been relatively successful in Southern Africa (Hayward et al. 2006; Hayward et al. 2007; Hunter et al. 2007). Yet, the ex-situ reintroduction of lions is largely disputed, with concerns that captive-origin individuals are deficient in species appropriate behaviours necessary for wild survival (Kleiman 1989; Hunter et al. 2013).

Reintroduction of species from wild and captive sources have had mixed results, with success ranging between 11% and 53% (Griffith et al. 1989; Beck et al. 1994; Jule, Leaver and Lea 2008). This method is becoming increasingly necessary, particularly for carnivores, within species conservation (Breitenmoser et al. 2001; Hayward and Somers 2009; Somers and Gusset 2009). Pre-release monitoring in ex-situ reintroduction allows selection of individuals most suited for release, thus increasing post-release success and survival (Biggins et al. 1999). Pre-release monitoring and training programs have increased the post-release survival of many species, including Golden lion tamarins (*Leontopithecus rosalia*) (Stoinski and Beck 2004), New Zealand robins (*Petroica australis*) (Armstrong et al. 2002), tamar wallabies (*Macropus eugenii*) (Griffin et al. 2001) and prairie dogs, (*Cynomys*) (Shier and Owings 2006). One factor that is known to result in reintroduction failure is that captive individuals are behaviourally inept for survival within challenging environments (Watters and Mehan 2007; Jule et al. 2008). Through the study of animal personality, we have the ability to

identify key species-specific behavioural traits necessary for survival, allowing us to prepare animals and identify individuals that are most suited for release (Watters and Meehan 2007).

Animal personality is the behavioural differences between individuals which can be relatively consistent across contexts (Dingemanse et al. 2009; R  ale and Dingemanse 2010).

Personality influences interactions and group structure, (Watters and Powell, 2011), while a personality trait may or may not be expressed by all individuals of a species (R  ale et al. 2007). Boldness is a trait that is important for individual and species survival and adaptation (Bremner-Harrison et al. 2004). How boldness impacts dominance and social structures, other behaviours (such as aggression) and responses to predators have been explored in various species (wolves, *Canis lupus*, MacDonald 1983; three-spined sticklebacks, *Gasterosteus aculeatus*, Ward et al. 2004; field crickets, *Gryllinae*, Kortet, Rantala and Hedrick 2007; crayfish, *Pacifastacus leniusculus*, Pintor, Sih and Bauer 2008; domestic cats, *Felis catus*, Finkler and Terkel 2015). Boldness is one trait that has received the most focus in personality research in the context of reintroductions (Bremner-Harrison et al. 2004; Watters and Meehan 2007; Sinn et al. 2014). Within ex-situ reintroduction programs, assessing boldness has been found to be effective in predicting post-release survival.

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.

Conversely, Sinn et al. (2014) found the opposite for Tasmanian devils (*Sarcophilus harrisi*), with individuals who survived post-release were up to 3.5 times bolder than those that perished. These studies used novel stimuli in the evaluation of individual boldness by recording behavioural responses to unknown objects (coloured balls, boxes, mirrors and unfamiliar human). Elliot et al. (2014) investigated lion dispersal within wild prides and suggested that a transient male that displays reduced locomotion could be considered bolder than one that exhibits solitary dispersal. This is due to larger male coalitions have a higher

chance of becoming dominant over a pride compared to solitary males. However, the application of novel stimuli and investigating pride dispersal in the evaluation of a pride of African lions within an ex-situ reintroduction program was not appropriate. Playbacks are a non-invasive technique which have been previously used to assess wild lion responses, with the purpose of establishing population densities (Ogutu and Dublin 1998; Cozzi et al. 2013; Omoya et al. 2013) and territorial responses at a kinship (Spong and Creel 2004), sex, age, individual, and pride level (McComb, Packer and Pusey, 1994; Grinnell and McComb, 1995; Heinsohn and Packer, 1995; Heinsohn, Packer and Pusey 1996; Heinsohn, 1997). From these studies, we know that lions will react to amplified pre-recorded vocalisations of unfamiliar conspecifics, competitive, and prey species. Responses of these studied lions indicate that they are capable of evaluating the number of vocalising intruders and respond accordingly; response corresponding with the presence and absence of other pride members, such as adult male(s), adult female(s) and cubs. Through the use of playbacks, we intended to investigate boldness of a pride of captive-origin African lions by recording individual behavioural responses to stimuli.

Within reintroductions, cohesion of social groups have proved to be a vital component which can contribute to post-release survival of various species, including wolves (*Canis lupus*) (Somers and Gusset 2009) and African wild dogs (*Lycaon pictus*) (Gusset, Slotow and Somers 2006; Somers and Gusset 2009). Of the various behavioural traits, social behaviours are viewed as highly flexible, as the behaviour of an individual is impacted upon by the interactions shared with conspecifics (Montigilo, Ferrari and R  ale 2013). Investigating personality on a social species allows us to assess whether individuals within a group vary in their degree of specialisation (R  ale and Dingemanse 2010), while the social roles of individuals can be established (Montigilo et al. 2013). Social role refers to the tactic or behaviour used by an individual in response to challenging social circumstances, such as

competition for food, mates and space (Bergmüller and Taborsky 2010; Montiglio et al. 2013). Keystone individuals have the ability to influence the social environment, by manipulating interaction frequencies and social roles of other individuals (Montiglio and Ferrari 2013). As a social species, lions express species-specific affiliative interactions, where variations in social interaction frequency have been identified within wild (Schaller 1972), captive-origin (Dunston et al. 2016) and zoological (Matoba et al. 2013) prides. Social network analysis (SNA) facilitates assessment and quantification of pride composition (Sih et al. 2009; Krause et al. 2007) and the intrinsic and extrinsic influences which impact social organisation (Crook et al. 1976). Abell et al. (2013a) conducted the first SNA upon a lion pride of captive-origin, concluding that the pride was socially cohesive, while identifying a keystone adult female, and the various roles of adults and cubs in pride sociality. Whether aspects of lion sociality and social roles correlate with other natural behaviours and boldness is currently unknown.

The natural behaviour of wild lion prides has been well established. Described as a highly inactive species, Schaller (1972) observed resting behaviour to average 20-21 hours a day with peaks of activity occur prior to 0800 hr and post 1700 hr. As opportunistic hunters, lions prey upon various species (Davidson et al. 2013) and when possible, will scavenge (Packer et al. 1990). Hunting is predominately conducted by females, while males will assist when pursuing large prey species, such as buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*) or elephants (*Loxodonta*) (Funston et al. 1998). Within captivity, the expression of these natural behaviours are often inhibited (Shier and Owings 2006), with the captive environment being predictable and unchanging (McPhee 2004). Regardless of the provision of complex environments, captive felids are often at risk of developing obesity, inactivity and stereotypies (Altman 2005). The effect of a captive-origin upon the daily

activity and hunting ability of a pride located within a fenced reserve and allowed to become self-sustainable is currently unknown.

Behaviour, sociality and boldness are important factors that are likely to determine post-release success of individuals and prides. By assessing these three aspects, we are able to further our understanding of the role of individuals within a pride. In addition, we aim to examine whether relationships, at a pride and individual level, exist between these behaviours. This will allow us to identify within pride personalities, which, if found to be linked to post-release survival, will assist in future animal selection and management of ex-situ reintroduction programs. The aim of our study is therefore to further develop the methodological tools to measure aspects of behaviour, with a focus on sociality and boldness, and initiate the exploration for stable relationships between these behaviours. This study is intended to explore if lion personality may be of value to researchers assessing prides in future ex-situ reintroduction programs.

Methodologies

Our pride is managed by the African Lion and Environmental Research Trust (ALERT), who, in conjunction with partner organisations, operate an ex-situ reintroduction program, aiming to conduct releases of prides and coalitions into the wild (Abell et al. 2013b). The pride was located within a 403 acre fenced managed reserve with GPS coordinates 19°30'S, 29°44'E (Figure 1). The reserve is situated on the central Midlands plateau within the Zambebian Highveld eco-region and terrestrial Zambebian biogeographic zone (Abell et al. 2013a). During the study, the reserve contained naturally occurring prey species (common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*)) and introduced species (impala (*Aepyceros melampus*) and plains zebra (*Equus burchelli*). We studied the pride between the 27th of August and 22nd of September 2013. The pride consisted of 1 adult male (MI) and 5

adult females (AS, NL, KE, KW, PH) who were of captive-origin, and their 1 sub-adult male (AS5) and 4 sub-adult female (AS4, AT1, KE3, KE4) wild born offspring.

Behavioural measures were collected via direct observations from a research vehicle the pride was habituated to. Observations were conducted up to thrice daily during fixed times; 0630-0830 hr (session 1), 1100-1300 hr (session 2) and 1600-1800 hr (session 3). Data was collected on an individual basis for activity budgets, social interactions, hunting behaviour and boldness.

Activity budget:

Through the use a species specific ethogram (Supplementary Material Table 1), we collected an activity budget each time the pride was observed. Via scan sampling, each lion was identified and their behaviour recorded every five minutes. The duration of which an activity budget was collected over in any session ranged between 1-2 hours. All other behaviours were collected simultaneously with the activity budget, at all occurrences.

Social interactions:

Social interactions were recorded via all occurrence sampling. Interaction types were categorised as greet, groom, play and aggression, previously described by Schaller (1972). The interaction type, lion who initiated and received, and whether the interaction was accepted, ignored or rejected was recorded. A social interaction bout was considered to have ceased once the interaction was not observed for more than one minute. For encounters where more than one interaction type was observed, only the initial behaviour was recorded, avoiding pseudo replication.

Hunting behaviour:

Hunting behaviour were recorded via all occurrence sampling, and were categorised into kill and chase behaviour. Kill behaviour involved finding lions to have physical signs of having killed and fed (extended stomachs, blood on the body and or the presence of a carcass). The

prey species (if identifiable), the pride members who exhibited signs of having fed, and an estimated time of the kill were recorded. Chase behaviour involved observing the pride to hunt a prey species, were the prey, the pride member(s) who initiated and participated in a stalk and or chase, the direction of approach (ambush, direct, left or right flank) of each lion, whether contact and a kill was made, and partakers of carcass consumption were recorded.

Boldness test:

Two boldness tests were conducted during the study; one consisting of territorial vocalisation of approximately 8 unknown conspecifics, and the other consisting of feed calls of approximately 4 spotted hyenas (*Crocuta crocuta*). Each playback was conducted during the last 40 minutes of the third time session (1600-1800 hr). Each playback type was played once for the pride during the study, where 15 days separated the tests. The duration of the lion playback was 180 seconds, and the hyena playback 220 seconds. The playbacks were saved as wav files on a USB portable device, which was then connected to and amplified through 2 portable speakers, 1800 W Superman Professional Speakers (frequency response AC220-240v, 50-60Hz). The speakers were situated vertically in the back of a utility vehicle, which was positioned outside the reserve boundary, a minimum of 200 metres from and out of view of the pride. Upon commencement of the playback, the reactions of all visible lions were recorded. A +1 score was associated with a bold response, such as approach and seeking an elevated position, and a -1 was associated with fearful response, such as retreat and hiding behind objects within the environment. All response types recorded and their associated scores are detailed in Supplementary Material, Table 2. The responses of the lions were recorded for up to 30 minutes, or ceased once all individuals stopped their approach or retreat, and conducted behaviours that indicated interest had terminated (eg. resting or grooming) for more than five minutes. At the completion of each test, we calculated a

boldness score per individual lion, with a low score (minimum of -7) indicating a more fearful individual, while a higher score (maximum of 13) indicating a bold individual.

Statistical analysis

The pride was observed for a total of 94 hours, which were conducted over three session times: 38 hours for 0630-0830 hr, 29 for 1100-1300 hr and 27 for 1600-1800 hr. The activity budget was analysed using statistical package SPSS, Version 20 (IBM Corp. 2011). Firstly, behaviours were calculated to provide an average percentage of time observed conducting the behaviour. Discrete Pearson correlations assessed relationships between three activity budget behaviours (resting, alert, direct movement (M1) and exploratory movement (M2)) and age. As our data was normally distributed, repeated measures ANOVAs assessed for whether resting or alert behaviours significantly varied across the three observation session times.

We collected a total of 485 social interactions over the 94 hours, which were standardised on a pairwise and hour basis. Interactions were compiled into directional, weighted matrices for greet, groom, play, aggression and all social interaction types. All matrices were then analysed via social network analysis (SNA) statistical program UCINET, version 6.543 (Borgatti et al. 2002). For each network, we generated density, degree (indegree and outdegree), betweenness centrality and clique groups. Density of a matrix is the proportion of all possible connections within a network, with a high value (1) indicative of a highly connected network, and a low value (0), an unconnected network (Wasserman and Faust 1994; Wey et al. 2008). Degree is the number of direct connections an individual has with others within a network; indegree describes the interactions received, while outdegree describes the interactions initiated by an individual (Wey et al. 2008; Sih et al. 2009). Symmetrical matrices for interactions were compiled prior to calculating betweenness and cliques. Betweenness measures the centrality of an individual within a network, evaluating

the number of shortest paths that are required to be passed through prior to reaching a target individual. A more central individual has a higher value, and connects other group members and subgroups which may not be directly connected (Krause et al. 2007; Croft et al. 2008; Wey et al. 2008). A clique is a sub-group of nodes which are directly connected to each other (Wey et al. 2008). UCINET generated normalised indegree and outdegree which were then tested through a Spearman's rank correlation in Genstat 17th Edition (VSN International 2014) for dependence within and between networks via a Spearman's correlation. A Kendall's tau correlation (conducted in GenStat) was conducted to examine whether associations between social influence (degree) and social power (betweenness centrality) occurred within and between networks (Abell et al. 2013a). NETDRAW, version 2.1476 (Borgatti et al. 2002) provided visual representations of associations within each network in the form of sociograms and cliques. As matrices were directional, line thickness illustrates the strength of associations between lion pairs, where a thicker line indicates a stronger association (Croft et al. 2008). Arrows within the sociograms indicate the direction of interaction between lion pairs (Wey et al. 2008). A Mantel test evaluated the significance between each social network and age, gender, kinship and a random network (generated in UCINET), using SOCPROG version 2.4 (Whitehead 2009). This analysis compared matrices collected upon the same individuals, with the null hypothesis that no relationship between the two matrices existed (Abell et al. 2013).

Hunting behaviour was calculated to the percentage frequency individual lions were observed to conduct stalk (total of nine counts) and consumption (total of seven carcasses located) behaviours. Two boldness were conducted, one using a conspecific territorial vocalisation playback and the other, the feeding vocalisations of a group of spotted hyenas. During the conspecific playback, only the 5 adult females (AS, NL, KE, KW, PH) and 1 sub-adult females (AT1) were observed and their responses recorded. For the spotted hyena playback,

the entire pride was present and responses recorded. Boldness scores were calculated for each lion from their response types using, Supplementary Material, Table 2.

To assess for significance between the various aspects of behaviour, we conducted Spearman's correlations between boldness scores, average percentage daily activity, social influence (in and outdegree) and power (betweenness centrality), and hunting behaviour, using GenStat 17th Edition (VSN International 2014).

Results

Activity budget:

Resting behaviours ranged between 51.69% (MI*^m) and 68.98% (KE*^f), with an overall pride average of 60.91% (Table 1) of total time observed. Alert behaviours ranged between 8.51% (MI*^m) and 24.22% (KE4), with an overall pride average of 16.62%. A negative correlation between age and alert behaviours ($r = -0.928$, $N = 11$, $p < 0.001$) indicate that sub-adults were most likely to be alert than adults. Session time was found to have a significant effect on pride behaviour. Resting significantly differed between the three time periods ($F_1 = 1725.325$, $p < 0.001$), with a peak in behaviour during session 2 (1100-1300hr; 70.94%), compared to sessions 1 (0630-0830hr; 50.19%) and 3 (1600-1800; 62.23%). Alert was found to significantly differ between sessions ($F_1 = 124.846$, $p < 0.001$), with a higher percentage of this behaviour observed in session 1 (Table 4). Lions were out of sight and not present for an average of 2.06% and 15.47% respectively, with adult male MI* observed to be mostly likely absent (33.50%). Adults spent significantly more time conducting direct movement (M1) than sub-adults ($r = 0.623$, $N = 11$, $p = 0.041$). Exploratory movement (M2) was the most performed locomotion for all pride members, except for adult female KE. All lions were observed to stalk prey (M3), while only six members (KW, NL, KE, AT1, KE3 and MI) engaged in a chase (M4). Self-grooming, eating and social behaviours were observed for all lions, with pride

means of 1.22%, 0.27% and 0.62%, respectively. Vocalisations were conducted by six lions (AS, KW, PH KE, KE4 and MI), with an average of 0.07%, while abnormal behaviours were observed for five pride members and ranged between 0.08% and 0.25% (mean of 0.05%).

Social interactions:

Greet and all social density measures, 0.818 and 0.909 respectively, indicate that the pride was highly connected. For the remaining networks, density was low, (groom = 0.409, play = 0.309, aggression = 0.164) indicating that some nodes were not fully connected in the corresponding network.

Sociograms for the greet and all social networks (Figure 2) indicate that all pride members were connected except for adult male MI and adult female NL. This is reflected in the low betweenness centrality values (Table 2) and lesser involvement in the cliques of these two individuals in the all social network.

Lions central to the greet network (Table 2) were detected in each of the four cliques (Figure 3). Adult male MI was found to be absent from this network (Figure 2), while along with adult female KW, had low centrality (Table 2).

Across the greet, groom and all social networks, an adult was observed to receive the greatest number of interactions (Supplementary Material Table 3). Conversely, a sub-adult or adult female NL were observed to initiate the greatest number of interactions, while adult male MI was least likely to initiate interactions within these networks. This was reiterated by the Spearman's correlation, which found greet indegree and outdegree to be negatively correlated ($r_s = -0.677, p = 0.022$).

Lions who received the most greet interactions (adults) were found to initiate the least play ($r_s = -0.690, p = 0.019$) and all social ($r_s = -0.767, p = 0.006$), but receive the most all social ($r_s = 0.740, p = 0.009$) interactions. Kendall's tau found groom betweenness centrality to be

positively associated with groom outdegree ($\tau = 0.4717, p = 0.020$), indicating that the lion's central to this network (females) initiated the most groom interactions. The Mantel test found the groom network to be positively associated with sex ($rM = 0.248, p = 0.030$), indicating a sex bias between females was present (Supplementary Material Table 4).

Sub-adults were observed to be the most connected and involved in the play network (Figures 2 and 3). This is reflected in the betweenness centrality values where all sub-adults had high values compared to adults (Table 3). Sub-adults were also observed to initiate and receive the greatest number of play interactions (Supplementary Material Table 3), with male AS5 most likely to receive and initiate play. Spearman's correlation found play indegree to be positively associated with play outdegree ($r_s = 0.736, p = 0.010$) and aggression indegree ($r_s = 0.715, p = 0.013$). Kendall's tau found play betweenness centrality to be positively associated with play indegree ($\tau = 0.610, p = 0.003$) and play ($\tau = 0.602, p = 0.003$), all social ($\tau = 0.381, p = 0.043$) and groom ($\tau = 0.442, p = 0.020$) outdegree. This indicates that pride members who were central to the play network (sub-adults) received the most play and initiated the most play, all social and groom interactions. The Mantel test (Supplementary Material Table 4) found the play network to be positively associated with full ($rM = 0.685, p = 0.002$) and half ($rM = 0.301, p = 0.018$) siblings.

Of the 24 observed aggressive encounters, 54.17% occurred during pride feeding. The remaining aggression was observed when adults were disciplining sub-adults (16.67%), disputed play between sub-adults (16.67%) and the unwanted presence of an individual between adults (12.5%). Discipline from adults towards young is expected, particularly from a mother, which was observed from most centrally connected (Table 2) KE towards her daughters KE3 and KE4. Adult female PH was also observed to be central to the network, however unlike KE who was observed to initiate and receive aggression, only initiated such encounters. Spearman's correlation found that pride members who initiated the most play,

also received the most aggression interactions ($r_s = 0.702, p = 0.016$). Kendall's tau found aggression betweenness centrality to be positively associated with aggression outdegree ($r_M = 0.420, p = 0.030$), indicating that those central to the network initiated the most aggression.

Hunting behaviour:

Hunting behaviour was investigated individually for hunting and carcass consumption. Zebra was the prey species which was observed to be most hunted (25%) and killed (18.75%) by the pride. Impala were found to be killed at the same percentage as zebra (18.75%). Although guinea fowl were subjects of hunts, no kills of this species were observed. One hunt of a duiker was observed and one scavenge feed was provided to the pride during the study. Adult were observed to hunt zebra (5.88%) and impala (23.53%), while sub-adults were observed to hunt zebra (47.06%), guinea fowl (17.65%) and duiker (5.88%).

Four pride members were observed to initiate a hunting sequence, at a mean of 4.81% of total hunts observed, while seven pride members were observed to join and participate in hunting sequences (mean of 4.28%). The pride was observed to conduct carcass consumption, with individuals participating in the behaviour between 6.82% and 13.64%, with a mean of 9.09%. A negative association was also found between those who participated in hunting behaviour and who were central to the aggression network ($r_s = -0.689, p = 0.019$). A negative trend between those who initiated hunting and all social interactions ($r_s = -0.528, p = 0.095$) and those who participated in hunting behaviour and initiated aggressive encounters ($r_s = -0.552, p = 0.079$) was also found.

Boldness test:

During the conspecific playback, only the adult females and sub-adult female AT1 were present and their reactions recorded. The spread of boldness test scores was not large, but adult female AS was determined to be most bold, while adults NL and KE and sub-adult AT1

least bold (Figure 4). A positive correlation was found between boldness and stalk hunting ($r_s = 0.705, p = 0.026$), due to adult female AS, who was most bold and likely to conduct this behaviour (Table 3). A negative trend between boldness and resting behaviour ($r = -0.494, p = 0.074$) was observed due to bold adult females AS and PH conducting lower levels of resting behaviour, and less bold KE, who rested at higher levels. Positive trends between boldness and alert behaviour ($r = 0.494, p = 0.074$) and vocalisations ($r = 0.548, p = 0.060$) were observed due to bold adult females AS (alert only), PH and KW (Table 4). A negative trend was found between boldness and greet ($r_s = -0.798, p = 0.057$) and all social ($r_s = -0.741, p = 0.092$) outdegree, due to bold females being least inclined to initiate these interactions (Table 4). PH was observed to lead the group towards the direction of the playback, however resulted in a lower boldness score than AS due to pausing during the advance.

The entire pride was present for the hyena playback, with adult females AS, KW and NL observed to be most bold, and sub-adult female AT1, adult male MI and adult female PH to be least bold (Figure 5). A positive association between boldness and M3 ($r_s = 0.705, p = 0.026$) was found, due to bold adult females AS and NL, and sub-adult male AS5 who conducted high levels of this behaviour (Table 4). A positive trend was observed between boldness and eating behaviour ($r = 0.581, p = 0.061$), due to bold adult female KW conducting high levels of this behaviour. A negative trend between boldness and direct movement ($r = -0.583, p = 0.060$) and aggression outdegree ($r = -0.579, p = 0.062$) was due to bold females AS and NL conducting lower levels of these behaviours, and less bold PH conducting higher levels (Table 3). Adults MI and PH were observed to approach the playback at a walking pace. NL was observed to lead the pride during the advancement, closely followed by the AS, KW and the sub-adult females.

Discussion

By observing various aspects of behaviour and conducting boldness tests, we were able to conduct intra-pride assessments and individual comparisons. Variations within and between behaviours highlight the varying roles of individuals, such as keystone and dominate individual(s), within pride sociality and hunting. Significant associations between boldness and stalk hunting movement and between hunting behaviour and social networks suggest the presence of behavioural consistencies.

We selected the two types of playbacks with anticipation that a variance in responses would be observed. The lion playback, expectedly, elicited a territorial response; adult females led the approach in the direction of the playback, continuously surveying the surrounding environment. The hyena playback, expectedly, elicited a competitive feeding response; the majority of the pride approached at a run in the direction of the playback, and proceeded to search and sniff surroundings. Playbacks of unfamiliar lions have been infrequently played to this pride, while vocalisations of captive lions (located approximately 1 km away) are regularly heard; however behavioural responses have not been previously collected intended to investigate individual boldness of this pride. It was unconfirmed whether the pride has been previously played feeding vocalisations of hyenas, however it is considered unlikely as no wild hyenas are known to occur outside of the reserve. Subsequently, we spontaneous responses of the pride to both playbacks, indicating that biological influences are likely. Responses were consistent with those observed for wild prides to lion playbacks (Heinsohn 1997; Heinsohn and Packer 1995; Spong and Creel 2004) and in reaction to competition with resident hyenas (Trinkel and Kastberger 2005; Watts et al. 2010; Périquet, Fritz & Revilla 2014). This suggests that captivity has not impacted upon the natural territorial and competitive responses of the pride to these stimuli.

Consistencies across boldness responses were observed, with adult female AS found to be most bold, NL to have a stable score (5), and sub-adult female AT1 to be least bold. Such

persistence in responses suggest the test protocol is appropriate for measuring boldness, while there is a possibility that a behavioural trait is present, however further replication is required. Considering boldness in conjunction with daily activity and social interactions, we are able to develop an understanding on the roles of individuals. Lioness AS was found to be ranked the highest, while PH was consistently low across the majority of the correlations. AS was most bold as this adult female led the pride advances towards the speakers for both boldness tests. It has been suggested that leadership and boldness could be correlated, due to both traits involving high risk (Johnstone and Manica 2011), while bolder individuals are likely to be dominant in social circumstances (Fox 1973, Macdonald 1983). Dominance between pride females can be difficult to ascertain due to a lack of a reproductive indicator; lionesses often synchronise oestrous and participate in crèche rearing of cubs (Packer, Pusey and Eberly 2001). Rudnai (1973) observed dominance between lionesses, which was determined by observing aggression while feeding and leading during pride hunts. AS received large numbers of social interactions from all pride members (Supplementary Material, Table 3), and along with high boldness and percentages of hunting behaviour and carcass consumption, we suggest that this indicates that this lioness is dominant. Whether AS would be persistently bold requires further replication, while observing successful hunts conducted by adult females would provide additional information that would assist in determining the dominance hierarchy of this pride.

Boldness scores of both tests were found to be positively associated with stalk hunting movement. This consistency was due to adult female AS in both tests and NL for the hyena playback, as these females were most bold in their responses and most likely to conduct stalk hunting movement. Consistency across the two tests suggest that an underlying behavioural trait may be present, however further replication is required for confirmation. Houser et al. (2011) observed that, prior to release, rehabilitated a cheetah (*Acinonyx jubatus*) exhibited the

highest frequency of hunting behaviour had the lowest success, and feeding and locomotion behaviours. Upon release this cheetah exhibited the least amount of movement and dispersal behaviour. Such behaviour could be expected to increase likelihood of post-release survival compared to those who disperse outside of protected areas. It is clear that behavioural traits could have an impact upon the survival of individuals post-release. The impact of the association between boldness and stalk hunting movement upon post-release success upon these lions is currently unknown. A full evaluation of individual behaviour and boldness prior to release and the implementation of post-release monitoring to record survival of released lions is required.

Associated trends between boldness and social and daily activity provide an indication into the varying roles of lions within age groups. The negative trend between boldness in response to the lion playback and resting behaviour indicate that bolder lionesses were likely to rest least, while a positive trend with alert behaviour indicates bolder lionesses were more alert. Such associations do not correspond with that observed within the activity budget analysis, as sub-adults were found to be significantly more alert, and rest the least. These associations were observed for this playback due to the small sample size (6) which contained only 1 sub-adult, and were not found for the hyena playback which included the entire pride. Boldness and initiated interactions (lion playback = all social and greet; hyena = aggression) were found to be negatively associated. For each interaction, these associations indicate that a bolder lion was least likely to initiate an interaction. This would be expected for the all social and greet interactions, as sub-adult female AT1 and sub-adult female NL were least bold and initiated higher frequencies of these interactions. Socially, NL was not observed to be dominant adult like AS and PH, however was a greater initiator of interactions (Supplementary Material, Table 3). AT1 was less central to the groom and play networks, possibly due to the absence of her mother and no full siblings within the pride, unlike the remaining sub-adults who had strong

connections with their mothers and siblings. Adults MI and PH accounted for the negative trend between boldness (hyena playback) and initiated aggressive encounters (Supplementary Material, Table 3). This is an interesting association, as previous studies have found positive correlations between boldness and aggression (Sih, Bell and Johnson 2004; Bell 2005; Pintor et al. 2008). Brust and Guenther (2015) found boldness, measured by latency to approach a novel stimuli, and social aggression to be positively associated in both domestic guinea pigs (*Cavia porcellus*) and wild cavies (*Cavia aperea*). This allowed authors to assess the effects of domestication upon this behavioural syndrome; an area which would be of interest to apply to African lions within an ex-situ reintroduction program. Whether the tendency for a negative correlation between boldness and social aggression in captive-origin prides is persistent requires additional studies on this and other captive-origin and wild prides.

Evaluation of individual lion behaviour across boldness, sociality and hunting behaviour allowed roles and responses to be explored. Adult female PH was identified as a social keystone, due to high involvement and betweenness centrality in all networks, a discovery found previously by Abell et al (2013) and Dunston et al. (2015) for this pride. Keystone individuals have been identified to be important in social cohesion (Lusseau, David and Newman 2004), and are influential over group dynamics (Sih et al. 2009). Our social keystone exhibited interesting responses to the boldness tests. Although found to be bold during the lion playback, along with adult male MI, was least bold to the hyena playback. This suggests that this female is an individual who is likely to participate in territory defence against conspecifics, however, least likely to assist in scavenging a kill from hyenas. This is reiterated in the associations observed between hunt initiators and participants, and social networks. The pride members central to the aggression network (AS5, KE and PH) were least likely to participate in the observed hunts. This could be expected for sub-adult male AS5, while indicating at the possibility that adult females KE and PH are more likely to be

‘cheaters’ in pride hunts (Packer and Ruttan 1988). However, being peripheral to hunting behaviour does not devalue the importance of this individual within pride cohesion and survival. Rather it indicates the possibility of an age, sex (AS5) and social role (PH) influence may be occurring. This is particularly evident when considering the lower social role adult female NL, in conjunction with her boldness scores and hunting behaviour. Low boldness in response to the lion playback suggests that this lioness may not be influential in territory defence, while the high boldness in response to the hyena playback and higher participation in hunting behaviour suggests this lioness is more likely an active hunter (Packer and Ruttan 1988). Socially, NL has low centrality lacks a connection with adult male MI, perceived due to being spayed, previously discussed by Abell et al. (2013) and Dunston et al. (2015). Finkler and Terkel (2015) found intact domestic cats exhibited increased boldness; however a significant correlation between dominance rank and boldness was unable to be established, suspected to be due to this population having unstable social groups. Our SNA density results indicate that our pride is socially stable and cohesive, and associations with boldness indicate study with this focus is worth pursuing.

In relation to exhibiting natural behaviours, comparisons to wild prides indicate that our pride functions naturally. Lower levels of resting behaviour (52-69% of total time observed) were observed, compared to levels reported for wild (83-88%, Schaller 1972) and zoological lions (72-77%, Altman 2005). This was a result of two of our observation sessions (0630-0830 hr and 1600-1800 hr) occurring during known periods of activity; Schaller (1972) reported peaks of activity to occur prior to 0800hr and post 1700 hr. Our study also allowed us to focus on lion absence and presence during observations, finding that across the pride, individuals were absent an average $15.50\% \pm 1.98\%$ total time observed, with the adult male most likely to be absent (33.50%). Lion prides exist under fission-fusion societies, where pride members are often dissociate into sub-groups, which constantly change in composition (Schaller 1972;

Packer 1990), while adult male absence is a natural occurrence (Schaller 1972; Funston et al. 2003; Matoba et al. 2013). The differing roles of adults and sub-adults observed within network degree and centrality correspond with wild social behaviour observed by Schaller (1972). Hunting behaviour, despite a kill not being observed, indicates that the pride has become self-sustainable. The observed initiation and participation within the hunting of guinea fowl, zebra, impala and duiker of sub-adult females indicate that hunting behaviour is and continues to develop. Schaller (1972) observed cubs from 11 months of age to conduct stalking behaviour towards small prey species, prior to participating in pride hunts at two and a half years old. These consistencies to published wild prides suggest that the Ngamo pride exhibits natural levels of behaviour, indicating that a captive-origin does not impact daily activity, social and hunting behaviour.

Evaluation of daily activity, social and hunting behaviour, and boldness in conjunction with each other, suggests that behavioural consistencies exist within a captive-origin pride. This was the first study to investigate lion personality and highlight the potential this research has to assist conservation management programs. The non-invasive nature of our boldness test allow for replication upon captive, semi-wild and wild prides to occur, which will allow behavioural traits across prides to be explored while investigating for the effects of captivity upon personality. Information on the behavioural traits that allow pride construction, cohesion and survival will not only assist ex-situ reintroduction, but increase our understanding of lion personality.

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Compliance with Ethical Standards

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Conflict of Interest:

Author Emma Dunston declares that she has no conflict of interest.

Author Jackie Abell declares that she has no conflict of interest.

Author Rebecca Doyle declares that she has no conflict of interest.

Author Megan Evershed declares that she has no conflict of interest.

Author Rafael Freire declares that he has no conflict of interest.

Ethical Statement:

All applicable interactional, national, and institutional guidelines for the care and use of animals were followed.

Informed Consent:

Informed consent was obtained from all individual participants included in the study.

Figure Captions

Figure 1. Ngamo release site location.

* = captive-origin adult; f = female; m = male

Figure 2. Sociograms of calculated networks from observed social interactions. Symbols are nodes, which represent an individual lion. Node shape depicts the sex (circles are females, squares are males), while node size is proportionate to lion age; larger symbol represents an older lion. Line thickness between dyads are proportionate to the strength of association between a pair of lions; a thicker line indicates a greater frequency of interaction.

* = captive-origin adult; f = female; m = male

Figure 3. Cliques of calculated networks from observed social interactions. Triangles are cliques, while squares and circles are nodes, representing an individual. Node shape depicts the sex (circles are females, squares are males), while node size is directly proportionate to the age of the lion; a larger symbol represents an older lion.

* = captive-origin adult; f = female; m = male

Figure 4. Boldness scores of reactions to a conspecific playback.

* = captive-origin adult; f = female; m = male

Figure 5. Boldness scores of reactions of spotted hyena feeding calls playback.