Ex situ lion conservation

Behavioural responses to playbacks of competitors with focus on sex and age differences
Abstract
Due to increasing habitat loss, human-lion conflict, poaching and other reasons, African lion (*Panthera leo*) populations have suffered a drastic decline. The African Lion and Environmental Research Trust (ALERT) is working to stop this pattern and is the first organization with an ex-situ conservation project for lions. Before releasing lions raised by captive-bred adults, they must first be ensured to behave properly to make sure they have the highest chance of survival. One challenge in the wild is encountering and competition with unknown conspecifics. By conducting playback of unfamiliar lion roars, the behaviours of lions under this ex-situ reintroduction program were tested and compared with observations from earlier studies of wild lions. Social interactions were also collected and a social network analysis was done to give information about the social structure in the pride. This in turn was compared with boldness scores, calculated from behavioural responses in the playback experiments. Lastly, I searched for associations between age and sex with both boldness and social interactions.

The studied pride consisted of 12 lions. The lions were more vigilant when a playback consisted of numerous lions vocalizing, but playing more than three lions seemed to make them loose interest, suggesting either habituation or false information. One adult female and the alpha-male were most bold, followed by five sub-adults. Boldness did not vary according to sex or age differences, but the social network analysis showed that some social interactions were more dominated by one sex or age group. These behaviours were in agreement with comparisons of wild prides.

This study showed that captive-bred lions have developed natural social behaviours. Based on the behavioural responses observed by the captive-origin lions to the playbacks of unfamiliar lions, it is unclear whether these lions would appropriately respond when encountered with unfamiliar conspecifics in the wild post-release.

Keywords
Animal behaviour, Ex-situ conservation, Lions, *Panthera leo*, Playbacks, Reintroduction, Social network analysis

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1 Introduction

The African lion (*Panthera leo*) population is declining at an alarming rate. Over the past 21 years, between 1993 and 2014, the wild population has reduced by approximately 43% (Bauer et al. 2016). Today the population is estimated to be between 23,000 (Bauer & Van Der Merwe, 2004) and 32,000 (Riggio et al. 2013), but likely to be closer to 20,000 (Bauer et al. 2016). One of the major reasons for the decline is the habitat loss due to the growing human population (Bauer et al. 2015). Trophy hunting also contributes to the population decline. Because of the poaching of herbivores, which are food sources for lions, prey populations are declining across Africa (Craigie et al. 2010). This in turn has led to food depletion for lions, subsequently causing a decline in lion populations. The last major reason for decline is the human–lion conflict that has arisen because of the threat lions pose to livestock and human life. To protect livestock or as an act of revenge, local communities persecute and kill lions (Schulette et al. 2013).

1.1 Reintroductions

Due to the continuous population decline, both ex-situ and in-situ projects are working to prevent species from going extinct. Ex-situ management of animals, is a process aimed to protect them from threats by keeping them outside their natural habitat (IUCN, 2014). This could be done either by translocating wild animals from one population to another, or by using animals from captive-origin populations (ALERT, 2017). Examples of earlier successful ex-situ reintroductions of captive bred animals into the wild include amongst others the prairie dogs (*Cynomys ludovicianus*) (Sheir & Owings, 2006), the American red wolf (*Canis rufus*) (Philips & Parker, 1988), golden lion tamarins (*Leontopithecus rosalia*) (Beck et al. 1991), Arabian oryx (*Oryx leucoryx*) (Stanley Price, 1989) and New Zealand robins (*Petroica australis*) (Armstrong et al. 2002).

In reintroduction projects, animals can either be reintroduced through soft or hard release. A soft release strategy means that the animals will go through a pre- or post-release training to develop and express instinct and natural behaviour, also getting used to their new environment before being released (Kleiman, 1989). A hard-release does not include these conditionings and often leads to a failure of carnivore reintroductions (Abell et al. 2013). One of the reasons of failure from earlier ex-situ attempts with other species is that the released animals have not been sufficiently adapted to the wild environment (Watters & Meehan, 2007; Jule et al. 2008). Kleiman (1989) mentions important behavioural aspects that should be developed to improve survival when reintroduced. Two of these include being able to avoid predators and interact accurately with conspecifics.

There are no earlier attempts of ex situ reintroduction programs for lions. Although, there are commercial enterprises with lions, where lions are being cuddled and walked with by tourists to later on being released in an area for canned hunting (Big Cat Rescue, 2013). These kinds of organizations, mainly situated in South Africa, have nothing to do with conservation and are only money-oriented (Big Cat Rescue, 2013; Abell et al. 2013). This kind of practice is one of the reasons why serious attempts of ex situ reintroduction programmes have been declined (Abell & Youldon, 2013). Also, these projects are very expensive to run and some have seen them as an attempt of
failure, not spending the money on conservation of lions in the wild (Hunter et al. 2013).

Thanks to the earlier ex situ reintroduction programmes with other species it has been easier to identify the main factors for success (Abell et al. 2013). This study was conducted in the first ex situ reintroduction program for lions, with the aim to release lions raised by captive-origin ones. I will look at captive-bred and their semi-wild born sub-adult lions’ reactions when playing unfamiliar lion roars and compare their behaviours with those reported in previous studies of wild lions’ reactions.

1.2 African Lion & Environmental Research Trust (ALERT)
ALERT is working against the extinction of lions by implementing a model of conservation in Zimbabwe and Zambia (ALERT, 2017). One facet of program is the staged ex-situ reintroduction soft-release program of lions. The African Lion Rehabilitation & Release into the Wild Program is a three-staged program, aiming to reintroduce lions from a captive-origin into the wild. Firstly, the rehabilitation stage consists of captive-raised cubs between the age of six weeks and 18 months being walked in a private game reserve or national park. This encourages the development of natural behaviours by letting the cubs to interact with their environment, hunt prey species and do social bonding and play with their siblings. From the age of six months, tourists are allowed to join trained lion handlers on these walks, raising awareness and financing the project (ALERT, 2017). At 18 months old, it is no longer safe to take the lions for walks and are therefore retired and moved to the next phase of the rehabilitation phase, the Night Encounter program, where the lions can further practice improving their hunting skills.

Stage two is the release phase, where lions are released as a pride into large fenced wild area. Here, the purpose is for the lions to form a socially stable and self-sustaining pride where all human contact is terminated. Within this stage, they can live a normal life and hunt different prey species, but no other predators or conspecifics are present. In the Dambwa pride, all individuals are radio-collared to allow for observations of their movements (ALERT, 2017). During this stage, prides have had cubs which are never exposed to human contact. As these cubs are raised under a natural environment, they are subjects for release into national parks and protected game reserves (reintroduction phase) in the future once of appropriate (ALERT, 2017). To ensure the lions born into the release phase are well prepared for survival in the wild, long-term monitoring and assessment of behaviours must first be done to ensure that the lions exhibit natural behaviours.

1.3 African lions (Panthera leo)
A lion pride consists of three to six related female adults (though it can range up to 18), their offspring and a coalition of immigrant males (1–4) (Packer et al. 1988; Packer et al. 1991a). Lionesses are likely to stay in the same pride their whole lives, participating in cooperative hunting, territory protection and cub raising (Schaller, 1972). Males, however, leave their pride at young age, around two to three years old, to compete for a new pride and access to females (Bygott et al. 1979). Because of this, when faced with intruders, females and males compete for different resources; females mainly for their cubs and territory, while males for their females and the risk of being evicted from their pride (Schaller, 1972). Lions are classified to be cubs up until the age of two, sub-adults
between the ages of two and four years, and from the age of four they are classified as adults (Schaller, 1972).

Social mammals, like lions, need to cooperate to defend resources. When they encounter competitors, they should be able to consider the number of individuals that they would be able to interact with and at the same time assess the value of the resource (McComb et al. 1994; Maynard Smith, 1982). Packer et al. (1990) suggests that the main reason for lion sociality is because of the threat of conspecifics. Based on studies on wild prides in Serengeti National Park, lions can distinguish pride mates from strangers and also determine whether the pride is outnumbered by the intruders or not. Also, they seem to adopt a more careful approach when being outnumbered (McComb et al. 1994; Grinnell et al. 1995).

When wild lions are intruded by competitors, individuals will exhibit different behaviours. Captive bred animals have been tested on their ability to respond to competitors using playbacks of oral communications. For example, McComb et al. (1994) played single lions roaring and groups of three lions roaring in choruses to examine if lions in the focal pride would change their behaviours according to the number of lions in their own and the competitive group. The lions approached the loudspeaker more slowly when playing three intruders, also glancing back at their lagging companions and having a tendency of doing more pauses when approaching. Another response is roaring. Females do this if other pride lionesses are dispersed from the pride upon hearing the playback to recruit them for help (McComb et al. 1994). Males, however, do not take this into account as they instead seem to roar irrespective of the presence of other males (Grinnell et al. 1995).

Heinsohn and Packer (1995) studied the territorial responses of females to other females and showed that there are lagers and leaders in a pride. The laggards avoid the cost of fighting, staying behind their companions, while those that lead the pride take much bigger risks since most territorial fights often lead to death or severe injuries (Schaller, 1972; Packer et al. 1990; Packer et al. 1988). Female laggards could be termed either “conditional cooperators”, approaching when their help would contribute to higher chance of winning, “conditional guards”, lagging most when most needed and “unconditional laggards”, whom would not change their behaviour no matter the odds of winning a contest (Heinsohn & Packer, 1995). Behavioural responses of lionesses do not seem to be related to age and body size when it comes to territorial intrusion (Heinsohn & Packer, 1995). Neither do female lions show any apparent dominance hierarchy (Packer & Pusey, 1985). All this suggest that the fighting ability does not have to be related to the individual differences (Heinsohn & Packer, 1995).

Male laggards can also exist in a pride, but compared to females, male laggards do not change the grade of lagging when the odds of winning a contest with intruders change (Grinnell et al. 1995). However, lagging males seemed to approach more slowly, or not at all, in thicker cover (Grinnell et al. 1995).

Previous work indicate that female lions show an increased probability of approaching loudspeakers playing unfamiliar lion roars if sub-adults are present in the pride (McComb et al. 1994). This could either be because of the bigger need to protect their territory or because of the extra help for defense is present thanks to the younger lions (McComb et al. 1994). Since my pride consists of six sub-adults, I would expect the adult females to be defensive when playing the recordings.
1.4 Aims and hypotheses

The method used by McComb et al. (1994) was applied to study the behavioural reactions of a pride under the release phase of ALERT’s ex-situ program, intending to determine whether they would respond in a manner similar to wild lions. I set out to examine whether and how behavioural responses to vocal playbacks depend on the number of signaling and receiving lions. I predict that when the risk of losing would be greater than the chance of winning, the lions should not approach the loudspeaker. This would be when being outnumbered by the lions being played. When the lions in the pride outnumber the lions being played they should approach the loudspeaker, but more cautiously the larger the group of the lions being played are. When playing only one lion roar, I would expect the lions to approach the loudspeaker.

In this study, I also examined whether there are any behavioural differences depending on the sex of the lions being played and the sex of the lions in the pride. Males would risk losing their pride to an invading male, while also losing their entire lifetime reproductive success (Grinnell et al. 1995). I therefore hypothesize that the males in this study would approach the loudspeaker and become more defensive when playing male roars. I further predicted that their behavioural responses will not be as dependent on the number of females and younger lions present in the pride; instead they will be more dependent on the number of defenders (Grinnell et al. 1995). Females, however, are expected to adjust their decision to approach according to the composition of their group (McComb et al. 1994).

If the lions exhibited similar behaviours of those observed for wild lions, the work of ex-situ reintroduction could indicate that lions with a captive-origin are capable of developing a suite of natural behaviours, which could increase the chance of surviving in the wild, knowing how to approach and avoid competitors. This could show that playback experiments might be a successful method to use in other ex-situ projects.

Being a social animal, lions, just like humans, prefer some individuals more than others. A social network analysis can provide information of the social structure in the pride (Farine & Whitehead, 2015) and inform how lions are connected to each other in the network and in what way. By looking at different social interactions, relationship between boldness and sociality can be investigated and again also comparing sex and age differences. My hypotheses are that some lions are more connected to each other than to others and that there will be some differences in interactions, especially between the sub-adults and adults due to the age difference.

A positive result would be one step forward towards a release of the lions into the wild, since this study will provide information on a captive-origin pride’s behaviour prior to release when it comes to both behavioural responses and social behaviour. This is a contribution to the work of preventing the decline of African lion populations.

2 Materials and method

2.1 Study site

One of ALERT’s research sites is situated in the Dambwa Forest, Zambia (17°48’S, 25°51’N) (Figure 1), which is a government owned land leased by ALERT. The lions
that were studied are fenced within an area of 707 acres and can hunt prey species like puku (*Kobus vardonii*), impala (*Aepyceros melampus*) and duikers (*Cephalophinae*).

The pride consists of twelve lions, six adults and six sub-adults. Of the adults, one male and five females, were released into the release site in 2011, and in 2013 the first litter of cubs were born (two females and one male). In 2014 another litter of cubs were born (one female and two males) in the site to another female (ALERT, 2017) (Appendix A). At the time of the study, only the adult lions were collared with telemetry collars.

![Figure 1](image-url). The release site is situated in the Dambwa Forest, southern Zambia, close to the boarder of Zimbabwe (Google Earth, 2017).

### 2.2 Playback experiment
A BOSE SLIII speaker was used for the playback and was connected through Bluetooth to an iPhone where the mp3 files of the playbacks were saved. Playbacks consisted of unfamiliar lion vocalisations which differed in terms of numbers of lions and genders (one male, three males, three females, five, eight, thirteen and eighteen lions of mixed genders). One to two playbacks were done per week with at least five days apart, minimizing the risk of lions becoming habituated to playbacks. The speaker was located outside the fence and hidden in high grass, at a minimum distance of 200 meters from the lions. The playbacks were either conducted in the morning between 0800-1100 h or in the afternoon between 1500-1600 h when the temperature was not too high. All reactions were filmed with a Nikon Coolpix L330 until all lions had stopped paying attention to the recording or for a total of 30 minutes.

To quantify the boldness of each individual, they were given positive or negative scores ranging between -5 and 5 depending on their reaction of the playback (Appendix B). A high score indicated a bolder response, while a low score indicated a more fearful...
response. The total final score for each lion, when summarized the boldness for every treatment, was thereafter used for the comparison of sex and age differences. Also, for every minute spent active paying attention to the playback, each lion received a score. As with the boldness scores, these values were summarized and analyzed to see the effect of number of intruders, and how the sex and age of the lions differed in reactions.

2.3 Social interactions
The social interactions were recorded at all occurrences and included all grooming, greet, play and aggression, earlier classified by Schaller (1972). For each interaction, the initiator and receiver and whether it was accepted or rejected was recorded. If the behaviour was repeated or another one was initiated within one minute after the first one, it was not included in the analysis to avoid pseudo replication.

2.4 Statistical analysis
Eleven treatments were conducted, whereby two of them were replications of three males and thirteen lions. The total boldness and time score across all treatments for each lion was calculated to compare and analyze age and sex differences for social degree values, boldness and time scores. Since the behavioural response data was not normally distributed, the non-parametric tests Spearman’s rank correlation and two-sample Wilcoxon were performed using the statistical program R, Version 2.3-2 (Fox & Bouchet-Valat, 2017). To see the effect of number of intruders on boldness and time reactive to playback, the total boldness and time score for each treatment was summarized separately and analyzed using Spearman’s rank correlation (Fox & Bouchet-Valat, 2017).

A total of 104 social interactions were collected during eight weeks. All data were compiled into weighted directed matrices for all social interactions and the program Ucinet, Version 6.543, was thereafter used to do a Social Network Analysis (Borgatti et al. 2002). Density, degree and betweenness centrality analyses were done for all social interactions (groom, greet, play and aggression) and also for the total interactions (all social) to see which individuals that were dominating each network in the pride. Density values indicate how connected individuals are within the pride. A value of 1 indicates that all individuals in the network are connected to each other, while a value of 0 means no connection (Wasserman & Faust, 1994). The degree measures the activity level of an individual (Vital & Martins, 2009), where the in-degree score shows the level of receiving from other individuals, while the out-degree score represents the level of initiating (Wey et al. 2008). Betweenness centrality values indicate how individuals control or mediate relations between other individuals that are indirectly connected (Knoke & Yang, 2008). The higher the value of betweenness centrality is for an individual, the more it acts as a connector and mediator of interactions between unconnected lions within the network (Knoke & Yang, 2008). To test whether social interactions differed between males and females, a two-sample Wilcoxon test was conducted using R (Fox & Bouchet-Valat, 2017).

Sociograms for all social networks were generated using the program Netdraw, Version 2.147 (Borgatti, 2002). Sociograms provided an illustration of social networks, providing a clear indication of who interacts with whom and to what level. Each lion is represented by a node, which differs depending upon the sex (node shape) and age (node size) of the individual. Arrows connect individuals, showing the direction of the
interactions while line thickness showing the number of interactions between lions, with a thicker line indicating more interactions (Hanneman & Riddle, 2005).

3 Result

3.1 Playbacks

The playback experiment showed that adult female Rusha was the boldest individual in the pride (Figure 2), with a score of fourteen. None of the other adult females approached the loudspeaker, regardless of the sex or number of intruders on the playback. These other adult females were also observed to have shorter response times to playbacks, resulting in these individuals having the lowest scores, while sub-adult RS1 spent the most time being reactive, followed by her brother RS2 and mother Rusha (Figure 3).

The alpha-male, Zulu, was observed to only approach when playing males (one male and three males), but was more likely to be unresponsive to all other playbacks. During the second playback of three males, five lions were absent from the pride, including the oldest male sub-adult RS2. This was also the only time when Zulu started roaring when approaching the location of the speaker and after. All sub-adults except female RS3 approached as a response for some of the playbacks. For the lions that approached, they only paused on the way towards the speakers when playing three lions.

![Figure 2. Total boldness score for each lion across the eleven playbacks.](image-url)
The lions showed a higher probability of approaching when playing three males, but when playing more than three lions (five, eight, thirteen and eighteen) the likelihood of approaching dropped (figure 4).

There was no significant correlation between boldness and age ($r_s = -0.25, p = 0.43$). Also, a two-sample Wilcoxon test showed no relationship between boldness and sex ($W (9), p = 0.25$). Figure 5 shows the distribution of boldness scores with age as the independent variable. When testing for boldness scores and number of intruders no significant correlation was found ($r_s = -0.59, p = 0.074$). Time reactive decreased...
significantly with increasing number of intruders ($r_s = -0.722, p = 0.018$). A boxplot was created to visualize the distribution of time scores for each treatment (Figure 6). The probability of the lion to approach was independent of sex ($r_s = -0.40, p = 0.199$) and age ($W (10.5), p = 0.395$).

**Figure 5.** Boldness scores plotted against the age of the lions. Squares represent males and circles represent females. Individuals with the same age and boldness score are seen as one, but larger, shape. The triangle represents two individuals, one female and one male of the same age.

**Figure 6.** The time each lion spent reactive (minutes) for each playback treatment. All lions spent different amount of time paying attention to the playback and received a score for every minute. The black lines represent the median time for each treatment. Maximum and minimum time can also be read. The playback of five, eight and eighteen lions have outliers, again having values standing out from the other values because of some individuals being much more active than others.
3.2 Social interactions

The density values for greet, groom, aggression, play and all social were 0.30, 0.11, 0.04, 0.08, and 0.47, respectively. For all social interactions, the lion to initiate most interactions was Rusha, with an out-degree value of 1.73, while initiate least for all social were Zulu and Kwandi (0.18). The individual receiving most interactions for all social was Zulu (in-degree value 2.09) and those that received the least attention were the sub-adults RS3 and LE1 (0.36) (Appendix C). Rusha was also the lion with the highest betweenness centrality value of 8.08 for all social interactions and the lions with the lowest value was sub-adult LE3 (Appendix D). There were no significant correlations between boldness and any of the social interactions. The closest relationship found was between boldness and in-degree of all social interactions ($r_s = 0.541, p = 0.069$), suggesting that bolder individuals were likely to receive more social interactions. There was a significant positive correlation between grooming indegree and outdegree ($r_s = 0.88, p < 0.001$), indicating that individuals who initiate grooming are also those who receive the interaction. Initiating grooming behaviour was overrepresented by females ($W(29), p = 0.026$). Males received more aggression than females ($W(5.5), p = 0.041$). There was no significant difference for which sex initiated the most aggressive interactions. A significant negative correlation was found between age and play ($r_s = -0.66, p = 0.021$), indicating that the younger lions were still more playful than the adults. It was also the younger lions that received the most aggression ($r_s = -0.63, p = 0.028$).

The lions most central in the all social network were the ones that initiated most greets ($r_s = 0.66, p = 0.021$). Play betweenness centrality values were negatively correlated with being aggressive ($r_s = -0.59, p = 0.044$) and positively associated with play out-degree ($r_s = 0.67, p = 0.018$), which indicates that the lions most central to the play network were also the most playful individuals (the sub-adults). The lions most central in the groom network greeted the most ($r_s = 0.61, p = 0.037$) and received most grooming ($r_s = 0.75, p = 0.005$). Lastly, greet betweenness centrality values increased with greet in-degree ($r_s = 0.71, p = 0.01$) and decreased with play out-degree ($r_s = -0.69, p = 0.013$), suggesting that the lions most central in greet received most greetings but initiated play least of all.

The sociograms for each social interaction type are presented in figure 7, where the visualization of all social interactions (1) together indicate that the strongest connection was between Rusha and Zulu. There were also strong linkages between Rusha and Leya, LE1 and Zulu, and finally between LE3 and Zulu. The lion with least connections within the network was RS3, only seen interacting with five out of eleven lions.
4 Discussion

Rusha was the boldest individual in this pride and also had most social interactions in the network. At the same time, sub-adult RS3 was the lion with the lowest boldness score and had least interactions. Pike et al. (2008) explored the effect of social
interactions in an animal network in three-spined sticklebacks (*Gasterosteus aculeatus*), but had the opposite result. The boldest individuals were those having fewer interactions, while the shy individuals had more, but with a small number of group members. Even though no significant correlation could be found between boldness and degree in the present study of lions, it was still a close relationship between being bold and receiving interactions. A conclusion can therefore not be made that with a larger sample size and more data, a significant correlation between these variables would still not be found.

Interestingly, RS1 and RS2 spent the most time being reactive to the playback, followed by their mother Rusha. Even though they were not consistent in boldness throughout the playbacks, they both approached when conducted the first playback of three males. These three pride members had both the highest degree of receiving interactions, after Zulu, and also spent most time reactive to the playbacks. It is therefore possible that these sub-adults will become more like their mother as they become adults, being bold and protective when they have been released into the wild.

It was expected that Zulu would receive the most greets from the other lions, since he is the alpha-male and greeting him is a way of showing respect (Schaller, 1972). However, I found that initiation of grooming was female dominated in the pride. Schaller (1972) observed that grooming is a way of strengthening the social bond between adult females within the pride. Since males are not supposed to stay in the same pride their whole lives, as females do, it might not be as important for them than for the females. Female grooming behaviour can also be seen in several different primates (Henzi & Barrett, 1999). The reason why age was not correlated with grooming behaviour might be because the sub-adults are on the verge of becoming adults. The sub-adults were still more playful than the adults, which is expected since the younger the lions the more playful they are in the wild (Schaller, 1972). The lions in the pride were most aggressive towards the male sub-adults, but also to female RS1. It was not very surprising given that the sub-adults received most aggression, since the adults do this to discipline the younger pride members.

The focus on sex and age differences led me to the social network analysis, which is a good way of evaluating the social structure of a pride, while also providing important information when preparing for an ex-situ reintroduction. Before releasing the sub-adults, an individual’s role in a group must be known to help predict their success post release. These analyses can, and should, be done over a longer period of time to see if the structure changes and if so, establish a reason for these changes. By having a study conducted over time, each individual’s social role can be assessed for information of how important it is socially for the pride’s stability (McCowan et al. 2008; McCowan et al. 2011). Overall, sex and age did not affect how central an individual was in mediating and controlling relationships within the pride, and except for RS3 and LE3, the other sub-adults appeared to contribute to keeping the network together. This in turn might suggest that when reaching adulthood and post-release these lions will hopefully be capable of establishing a socially cohesive pride. RS3 and LE3, however, might not be as cohesive to their siblings when released, being candidates to become nomads. This can of course not be concluded, especially not from this short time of study, but from the look of their low betweenness values they might not stay together as close as the other lions after release.
Different studies suggest various explanations for variation in behavioural traits. These range from genetics (Van Oers et al. 2005) to life-history stage, individuals’ experiences (Sih et al. 2004; Réale et al. 2007; Dall et al. 2004) and also on maternal effects (Stamps & Groothuis, 2010). Yet, experience in life can make a consistent behaviour non-stable. Bell and Sih (2007) found a higher correlation between boldness and aggression in the threespined stickleback (Gasterosteus aculeatus) when have been exposed to predators. An association between being bold and aggressive has been reported in more species (Docterman & Jenkins, 2007; Duckworth & Badyaev, 2007; Johnson, & Sih, 2005; Kortet & Hedrick, 2007; Moretz et al. 2007). However, in the house cricket (Acheta domesticus), for example, no correlation could be found between boldness and being aggressive (Wilson et al. 2009). This was also the case in this study of lions, where no correlation could be found between boldness and aggressiveness. Having grown up in a safe environment with no threats around them, the lions, especially the bolder ones, might become more aggressive when encountered with unfamiliar conspecifics and competitors, like hyenas, in the wild.

As previously mentioned, experiences in life can change an earlier consistent behaviour (Bell & Sih, 2007). The future release into the wild of the six sub-adults means a big change for these individuals, with a completely new environment and challenges to face. The reactions shown by the sub-adults do not necessarily indicate that, when in the wild, they would exhibit the same level of boldness. It is also difficult to say who would have a higher chance of survival, since being a bold individual can both be beneficial and a disadvantage. In a study of captive-bred swift foxes (Vulpes velox), the individuals with the highest boldness score when captive were those with the lowest survival after release (Bremner-Harrison et al. 2004). The reason for this is probably because of the lower fear of approaching a novel object, or that bolder individuals are less likely to avoid intrusion of territorial conspecifics, predators and anthropogenic stimuli (Bremner-Harrison et al. 2004). On the other hand, boldness could be species specific since Sinn et al. (2013) showed that reintroduced Tasmanian devils that survived were 3.5 times bolder than those that did not. Being bold has also shown to increase the reproductive success in other animals, especially in males (Smith & Blumstein, 2008), coming to the conclusion that boldness is also a “trade-off” in fitness across different situations (Smith & Blumstein, 2008).

All adult female lions in this study, except Rusha, had a total boldness score of zero. Either the others were just not interested, or whether they might have known that Rusha is the one who would cover for them is unknown. These females could in that case be termed laggards, since those are the individuals not sharing equally in defending the pride as Rusha, a leader, would (Breed & Moore, 2011). Consistent behaviours make individuals predictable, which can be beneficial in a social group (Wolf et al. 2011). The response of an individual can be influenced of its group member’s earlier behaviour in a specific situation, and so, the laggards might act as they do because they know that their group members will take the lead and face the threat. In this pride, Rusha’s behaviour might was predictable to the other females, which could be one explanation for their lagging behaviour.

An earlier study did not find any relationship of body size and territorial responses of female lions (Heinson & Packer, 1995) and no measures were taken on the pride in Zambia to investigate this. However, Rusha is by far the largest female in body size and height, while Kela and Kwandi with the lowest boldness scores, are the smallest
lionesses. With a longer period of study and height measures of the lions, this would be interesting to see whether body size is associated with boldness.

When conducted the second playback of three males, the oldest male sub-adult, RS2, was absent and Zulu started roaring. Since three incoming males would be the biggest threat for males in a pride, it is possible that roaring in response to this playback was for calling RS2 to join for defense. Male lions often form coalitions that consist of either kinship or non-relatives (Packer et al. 1991b). The purpose of forming a coalition is for cooperation of keeping the access to females increasing their reproductive success and helping each other to protect their pride from incoming males to take over (Bygott et al. 1979). As RS2 gets older, it would be interesting to see whether he and Zulu would actually form an apparent coalition.

The non-significant difference in age for reactions to the playbacks indicates that the younger lions are not so dependent of their mother anymore as they are reaching adulthood. Heinsohn et al. (1996) studied juvenile lions’ reactions to playbacks of unfamiliar lion roars and the developmental responses between the age of eight and 42 months old. The result showed that when no adults were present, it was a 70% chance of approaching by the age of 37-42 months. Females showed a higher probability of responding with age, while males did not, but were seen most often in the back of the group when responding. The sub-adults in the Dambwa pride were never seen without adults when conducting the playbacks, since the pride usually stayed all together, and neither was there any difference between the sexes. Again, having almost turned four years old and considering the other juveniles were three years old, the sub-adults should be in the age of being bold enough to approach. The lack of time and replications also made it difficult to find any consistencies in boldness, making it impossible to come to a conclusion regarding boldness differences between the individuals.

Because the pride studied here usually stayed together, it was not possible to examine the effect of group size, which has been done for wild prides (McComb et al. 1994). Because of the bigger reactions when five individuals were not present (if this had to do with this or the fact that three males were played), a longer period of study might have allowed for looking at the changes of responses depending on the size of the pride.

McGregor (1992) proposed some of the problems with conducting playbacks to animals. The first problem is about the risk of habituation. When animals are exposed to the same sounds, and even different sounds but at the same or similar situations, they do tend to ignore them in the end or the reactions will not be as strong as during the first playbacks. The second and also more serious problem, is that the vocalizations being played might not mean what they actually were thought to. This study was designed to play territorial lion roars, but even though this was the search criteria when looking for the recordings, they might not have been perceived aggressive for the pride. The more playbacks that were done, the more the lions seemed to pay less attention to the playback, which could have been because of habituation. In nine out of ten playbacks, the lions stayed at the same location close to the fence, making it difficult to change the place to put the loudspeaker. This might have made the playbacks even less trustworthy towards the end of the experiment. Also, staying close to the fence might have affected their response in the way that they would feel more secure being protected behind the fence.

Neither sex nor age had any effect on boldness and time active to the playbacks, though the higher number of intruders being played increased the time active to it. But there
was only an increase until playing more than three lions and the following increase in number gave an unstable mean value of time scores. The low response of the lions when playing eight, thirteen and eighteen lions may be due to the possible confusion of the number of lions being played. As it is known about the lions’ ability to count the number of roaring intruders, they might also hear when it does not sound like a real pride. Earlier studies have only focused on playing maximum three lions at the same time (McComb et al. 1994; Grinnell et al. 1995; Heinsohn & Packer, 1995; Heinsohn et al. 1996). However, one of the aims in this study was to investigate their reactions when being outnumbered. The hypothesis was that they were not going to approach when playing more lions than the number present in the pride, which was true in this case, but looking at the time active to the playback it seemed as it was more a question of interest.

4.1 Conclusion

This study does not only provide information about a captive-origin lion pride, but also about lions’ social behaviours. The lions in the Dambwa pride did not really behave as expected when it came to playback experiments compared to wild lions. Although, the playbacks gave information on who was the boldest and least bold individual in the pride. These findings were then compared with their social behaviour, where bold individuals were more likely to receive social interactions from other lions and the opposite. Being more central in a specific network was associated with other social behaviours, and some social interactions were more dominated by a certain sex or age.

Social network analysis was a good method of exploring the current social structure in the pride. There was evidence of some individuals who preferred each other more than others and some were better in keeping the pride together socially than others. This should be followed up until the day of release to see if any changes occur and establish whether the individuals to be reintroduced are well-prepared. The differences in sociality associated with age and sex were mostly in agreement with what has previously been reported based on studies of behaviours of wild lions, indicating that captive-bred lions still display natural behaviours, which is of great importance when preparing for a release.
References


7. ALERT (2017). *Ex Situ Lion Conservation*. [http://lionalert.org/page/Ex_Situ_Lion_Conservation](http://lionalert.org/page/Ex_Situ_Lion_Conservation). Downloaded on **12 July 2017**.


5 Appendices

5.1 Appendix A - The lions

<table>
<thead>
<tr>
<th>Name</th>
<th>Sex</th>
<th>Birth</th>
</tr>
</thead>
<tbody>
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<td>M</td>
<td>8(^{th}) July 2008</td>
</tr>
<tr>
<td>Kela</td>
<td>F</td>
<td>3(^{rd}) May 2008</td>
</tr>
<tr>
<td>Kwandi</td>
<td>F</td>
<td>3(^{rd}) May 2008</td>
</tr>
<tr>
<td>Leya</td>
<td>F</td>
<td>26(^{th}) May 2008</td>
</tr>
<tr>
<td>Loma</td>
<td>F</td>
<td>26(^{th}) May 2008</td>
</tr>
<tr>
<td>Rusha</td>
<td>F</td>
<td>9(^{th}) August 2008</td>
</tr>
<tr>
<td>RS1</td>
<td>F</td>
<td>21(^{st}) June 2013</td>
</tr>
<tr>
<td>RS2</td>
<td>M</td>
<td>21(^{st}) June 2013</td>
</tr>
<tr>
<td>RS3</td>
<td>F</td>
<td>21(^{st}) June 2013</td>
</tr>
<tr>
<td>LE1</td>
<td>M</td>
<td>30(^{th}) January 2014</td>
</tr>
<tr>
<td>LE2</td>
<td>F</td>
<td>30(^{th}) January 2014</td>
</tr>
<tr>
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<td>M</td>
<td>20(^{th}) January 2014</td>
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5.2 Appendix B – Boldness scores

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</tr>
<tr>
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</tr>
<tr>
<td>Approach 10-20 m</td>
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</tr>
<tr>
<td>Approach 20-50 m</td>
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</tr>
<tr>
<td>Approach &gt; 50 m</td>
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<tr>
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</tr>
<tr>
<td>Retreats after &gt; 5 m</td>
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</tr>
<tr>
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</tr>
<tr>
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</tr>
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</tr>
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<td>Retreats after &gt; 50</td>
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</tr>
<tr>
<td>1-3 pauses</td>
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</tr>
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</tr>
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</tr>
<tr>
<td>Roaring</td>
<td>1</td>
<td>0</td>
</tr>
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</table>
5.3 Appendix C – Result for out- and in-degree values

Table 1. Out-degree values for all interactions. The higher value the more does the individual interact with others.

<table>
<thead>
<tr>
<th></th>
<th>Aggression</th>
<th>Greet</th>
<th>Groom</th>
<th>Play</th>
<th>All social</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zulu</td>
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<td>0.18</td>
<td>0.00</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
<td>Kela</td>
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<td>0.00</td>
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</tr>
<tr>
<td>Kwandi</td>
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<td>0.09</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
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<td>0.18</td>
<td>0.00</td>
<td>0.64</td>
</tr>
<tr>
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<td>0.64</td>
<td>0.09</td>
<td>0.18</td>
<td>0.91</td>
</tr>
<tr>
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</tr>
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<td>1.00</td>
</tr>
<tr>
<td>RS2</td>
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<td>0.91</td>
</tr>
<tr>
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<td>LE1</td>
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<td>0.82</td>
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<td>0.09</td>
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<td>LE2</td>
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<td>0.36</td>
<td>0.18</td>
<td>0.18</td>
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</tr>
<tr>
<td>LE3</td>
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<td>0.27</td>
<td>0.09</td>
<td>0.18</td>
<td>0.82</td>
</tr>
</tbody>
</table>

Table 2. In-degree values for all social interactions. The higher value, the more interactions does the individual receive from others.

<table>
<thead>
<tr>
<th></th>
<th>Aggression</th>
<th>Greet</th>
<th>Groom</th>
<th>Play</th>
<th>All social</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zulu</td>
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</tr>
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<td>0.73</td>
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<td>0.27</td>
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</tr>
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### 5.4 Appendix D – Result for betweenness centrality values

*Table 3.* Betweenness centrality values for four different social interactions and all together. Age and sex of the lions are also shown to more easily compare for the differences in social behaviours.

<table>
<thead>
<tr>
<th>Lions</th>
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<th>Sex</th>
<th>Groom</th>
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<th>Play</th>
<th>Aggression</th>
<th>All social</th>
</tr>
</thead>
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<td>Zulu</td>
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</tr>
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