Temporal modification of social interactions in response to changing group demographics and offspring maturation in African lions (*Panthera leo*)

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Abstract

In group living animals, affiliative social interactions maintain cohesion between individuals. Involvement in these interactions is likely to differ between individuals, depending on their sex, age and life history stages. Here we investigated different social network measures to describe greeting interactions within two prides of captive-origin African lions (*Panthera leo*). We aimed to determine if the introduction of cubs to these prides altered the strength of greetings networks among female lions. We also tested if the strength of greeting interactions changed between the age classes as younger lions matured. We found that interactions amongst female lions decreased from the period before cubs were born (least square means [95% CIs] 15.3 [7.67-22.93]) compared to after their integration into a pride (5.63 [-1.99-13.26] *χ*21 = 210.03, p *<* 0.001). In contrast, greeting network strength increased as offspring matured, with adults directing more interactions towards younger lions from 30 months of age (12.89 [1.96-23.82]) compared to when offspring were cubs (-0.69 [-11.63- -10.24] *χ*210 = 156.03, p *<* 0.001). We suggest that social interactions between age classes may mediate recruitment and dispersal in lion prides.

Keywords: African lion; dispersal; greeting; social interaction; temporal patterns

Abbreviations:

ALERT[[1]](#footnote-1)

1. Introduction

Sociality in mammals entails trade-offs between the benefits of group living such as increased success in locating resources, and the costs like increased competition for mates (Krause and Ruxton, 2002; Silk, 2007). When animals rely on associations with group mates to enhance their individual fitness, group cohesion is critical and requires individuals to coordinate their actions (Krause and Ruxton, 2002; Dunbar and Shultz, 2010). Cohesion between individuals is maintained by specific grouping behaviours, and often involves the formation and maintenance relationships through interactions. For example, allogrooming is a bonding behaviour for many species, like meerkats (*Suricata suricatta*) and ring-tailed lemurs (*Lemur catta*) (Kutusake and Clutton-Brock, 2010; Kulachi et al., 2015). Other species engage in greeting interactions which may be used to re-establish contact with group mates after periods of separation (*e.g.* the spotted hyena, *Crocuta crocuta*) or to establish contact before engaging in some other social behaviour (*e.g.* the African lion, *Panthera leo*) (Schaller, 1972; Glickman et al., 1997). Spotted hyena greetings involve two associates standing head-to-tail so that both parties may engage in olfactory investigation of the other’s ano-gential region (Glickman et al., 1997). Between lions, the greeting is performed when one lion bends its head toward another’s with contact lasting up to a minute (Rudnai, 1973). Although the interaction differs between the species, in both hyenas and lions there is evidence that the greeting interaction acts to reinforce social bonds amongst group mates (Smith et al., 2011; Matoba et al., 2013). Such species-specific interactions are often non-random in their occurrence and individuals can show preferences for conspecifics based on sex, body size or genetic relatedness (*e.g.* Abell et al., 2013a; Matoba et al., 2013).

Engaging in social interactions can be a time-consuming endeavour: allogrooming, a bonding behaviour for many primates, can occupy as much as 20 % of the day for some species (Dunbar, 1991). As time is a limited resource for animals, larger groups need to limit how long each individual spends interacting with group mates (Pollard and Blumstein, 2008). Therefore in many species, individuals form close relationships with specific group members, *i.e.* social bonds, which are characterised by a high amount of affiliative and a low amount of aggressive interactions and are stable over time (*e.g.* Silk, 2007; Silk et al., 2009; Schülke et al., 2010; Silk et al., 2010a; Silk et al., 2010b). As well as time pressures, members of larger groups face higher levels of competition and different classes of individuals are likely to be affected by competition in different ways (Quirici et al., 2011). Juvenile degus (*Octodon degus*) and the lesser kestrel (*Falco naumanni*) for example, are more likely to disperse from their natal group with increased habitat saturation (Negro et al., 1997; Quirici et al., 2011).

Amongst mammals, male-biased dispersal is the prevalent system enabling the males to access more mates, while females benefit from cooperation through kin selection and inherit high quality territories by remaining philopatric (Greenwood 1980; Silk, 2007). Sex-biased dispersal is a means of avoiding competition with kin so if dispersal is inhibited, the frequency of competition among individuals who are unable to disperse and the philopatric sex increase (Greenwood, 1980; Komdeur, 2010). Amongst members of the philopatric sex however, the development of social bonds is expected to reinforce against dispersal (Lawson Handley and Perrin, 2007). Support for this comes from studies like that of Harris and White (1992) who found that female red fox (*Vulpes vulpes*) cubs who had their ear tags chewed more during grooming were less likely to disperse. Similarly, dispersing blue monkeys (*Cercopithecus mitis stuhlmanni*) and yellow bellied marmots (*Marmota flaviventris*) have weaker social ties with natal group members than philopatric individuals (Ekernas and Cords, 2007; Blumstein et al., 2009).

African lions live in groups, called prides, of related adult females who raise their offspring communally and represent a socially stable unit (Schaller, 1972; Packer, 1986). Group living for females provides enhanced defence of long-term territories and communal protection of offspring, with larger prides achieving greater reproductive success (Packer et al., 1990; Mosser and Packer, 2009). For males, grouping enables the formation of coalitions that compete to oust resident males for access to female prides (Packer et al., 1988; Pusey and Packer, 1994).

Females keep cubs hidden until they are 4-8 weeks of age with full integration into the pride being a gradual process (Schaller, 1972; Packer and Pusey, 1983). The presence of cubs can cause the formation of sub-groups, which can lead to pride fission as non-lactating females may have limited contact with mothers during this time (Schaller, 1972; Packer, 1986). However, whether the presence of cubs alters interactions among lionesses whose pride remains intact is unclear (Matoba et al., 2013).

Sub-adults disperse in cohorts, or groups that comprise individuals born to the same pride within 18-months of each other (Pusey and Packer, 1987). The timing of natal dispersal is influenced by the age and sex of a sub-adult, but is overwhelmingly determined by the arrival of extra-pride males (Hanby and Bygott, 1987). While young males are always evicted by unfamiliar males, female sub-adults will remain if they are sexually receptive (Hanby and Bygott, 1987). However, female dispersal does occur when a pride surpasses it optimum size (3-6 females in open grassland systems, 3-11 in woodland environments) especially in times of low prey abundance (Pusey and Packer, 1987; VanderWaal et al., 2009).

In this study, we used greeting interaction data from an ex-situ lion reintroduction programme (The African Lion and Environmental Research Trust (ALERT)) which aims to release the offspring of captive founders into the wild (Abell et al., 2013b). We investigated whether the integration of cubs into prides altered social network measures of greeting interactions among female pride mates. We recorded greeting frequencies amongst females in two time periods (prior to the birth of any cubs and following the integration of a cohort into a pride). As the inclusion of cubs increased the number of social partners available to each lion, we expected the strength of networks to decrease in the second period. However, we also wanted to know if any change to the strength of greetings could be attributed to females with or without cubs. Previously, social network analysis (SNA) confirmed that mothers have strong associations with their cubs and that individuals preferentially interact with kin (Abell et al., 2013a). We therefore predicted that mothers would interact more with their young, leading to weaker network strength for mothers amongst adult individuals than those lionesses without young.

Our second aim was to determine if greeting networks were altered as offspring approached independence. Specifically, we wanted to know what age offspring-adult greeting interactions changed and if a particular demographic initiated the changes. We used a sample of greetings from a period when a pride’s cohort were all under 18-months of age and classified as cubs (*e.g.* VanderWaal et al., 2009). We compared this network to a continuous series of three-month periods throughout sub-adulthood (18-48 months (Pusey and Packer, 1987). We expected greetings to increase between adult and sub-adult females as the philopatric sex (Lawson- Handley and Perrin, 2007). For male sub-adults, we expected that social cohesion with female pride mates would play a less important role and greetings between adult females and maturing males would decrease. However, if males are resident when their sons reach maturity, there is evidence of fathers forcing their sons to leave, of male sub-adults apparently leaving voluntarily and of sons emigrating with their father/s to become residents in a new pride (Packer and Pusey, 1982; Pusey and Packer, 1987). As larger coalitions improve male reproductive success, we expected that lone mature males would recruit their maturing sons into a coalition resulting in an increase of greetings between older and younger males (Pusey and Packer, 1987).

1. Methods

2.1 Study sites and animals

The study was conducted from September 2010 to February 2015 in the Ngamo release site, near Gweru, Zimbabwe, and September 2011 to July 2016 in the Dambwa release site, near Livingstone, Zambia. Both sites are surrounded by boundary fence lines. The Ngamo site spans 1.63 km² and consists of areas of open grassland and dry miombo (*Brachystegia*) woodland. Two small antelope species (common duiker *Sylvicpra grimmia* and steenbok *Raohicerus campestris*) occur naturally in the area and introduced prey species (impala *Aepyceros melampus*, wildebeest *Connochaetes taurinus* and plains zebra *Equus burchelli*) were available to the pride at various stages over the study period (Abell et al., 2013a). The Dambwa release site is 2.86 km² with vegetation ranging from grassland to woodland. The common duiker occurs naturally and introduced species (impala, eland *Taurotragus oryx*, puku *Kobus vardonii*, Defassa waterbuck *Kobus ellipsiprymnus defassa*, wildebeest and plains zebra) were also present in the site at various periods of the study. Although prey populations were available to the lions, both prides were provided with supplementary feeds during periods of low prey density.

The Dambwa and Ngamo prides both comprised one adult male and six adult females. One female from both prides was removed from their respective sites over the course of the sub-adulthood analysis period, and so were not included in this part of the study. The Ngamo pride was released into the site in August 2010 and had four female and one male offspring from three litters. The Dambwa pride was released in August 2011 and had three female and three male offspring from two litters. Following the birth of cubs, deslorelin contraceptive implants were used on all reproductively able females to down-regulate reproduction. To maintain contraception, females were implanted at 24-month intervals as recommended by Bertschinger et al., (2008). Because females may start mating as early as 24-months old (Packer et al., 1988), implants were also used on the prides’ female offspring from 20-22 months of age to prevent inbreeding.

2.1.1 Data collection  
Data collection was carried out by ALERT’s trained research technicians as part of regular monitoring of the prides following their introduction into the sites. Research technicians entered the sites in vehicles for periods of two hours up to three times a day during the hours: 0630-0830, 1100-1300 and 1500-1700 in the Ngamo site, and 0700-0900, 1030-1230 and 1500-1700 in the Dambwa site. Lions were individually identifiable by research technicians who collected greeting interaction data *ad libitum*. When a greeting was observed the date and time along with the initiator and recipient of the interaction was recorded. For this study, only greetings that were tolerated by the receiving lion were used to represent affiliative interactions among pride mates (n=8870).

2.1.2 Data preparation

To investigate if the integration of cubs into the prides affected the strength of social networks among adult females, we only used greetings that occurred between these individuals in both prides. We identified a phase in each prides’ data set prior to the birth of cubs (Dambwa: 1-Nov-2012 to 29-Mar-2013; Ngamo: 4-Sep-2010 to 1-Dec-2010). A second phase was also identified after a pride’s cohort had been integrated but were all under 18-months old and therefore classified as cubs (Dambwa: 5-Sep-2014 to 3-Nov-2014; Ngamo: 20-Apr-2012 to 20-Jun-2012) (*e.g.* VanderWaal et al., 2009).

Natal dispersal occurs over a wide age range (20-65 months), possibly due to the unpredictable nature of pride takeovers (Hanby and Bygott, 1987; Elliot et al., 2014). However, following Pusey and Packer (1987) we defined sub-adults as ranging in age from 18-48 months. Because aggregating data over long periods can hide patterns in interactions (*e.g.* Rubenstein et al., 2015), to investigate greetings over sub-adulthood among all pride members, we first created a ‘cub’ phase, when all offspring were under 18-months. We then grouped greetings into three-month periods starting from the point that the oldest litter in a cohort turned 18-months old.

2.1.3 Social Network Analysis

For both analyses, greetings were organised into weighted edgelists for analysis in the R (R Core Team, 2016) SNA package *tnet* (Opsahl, 2009). We calculated the direct metric strength (indegree for received interactions, and outdegree for initiated interactions) and the indirect metric betweenness for each lion. Strength is the number of social partners an individual has, weighted by the frequency of interactions that occur between a focal individual and each partner (Formica et al., 2016). Betweenness incorporates indirect connections and measures the number of shortest paths between every other pair of animals in a network on which a focal animal lies (Wey et al., 2008).

2.1.4 Model selection and building

We used the R package *lme4* (Bates et al., 2015) to build linear mixed models (LMMs) for strength and betweenness values for all networks. For female greeting models we used the fixed factors phase (pre- or post-cub) and if a female was a mother, or not. For sub-adult maturation periods, models included the fixed factors age class (cubs = < 18 months of age, sub-adults = 18-48 months, adults = > 48 months), phase (cub, or sub-adult average age) and sex. We also built a series of sub-models using only adult-directed greetings towards sub-adults, or vice versa. This was to allow us to examine if a particular age class or sex was more active in causing any changes in greetings. These models also used the fixed factors age, phase and sex. To assess multicollinearity between fixed factors, variance inflation factors (VIFs) were obtained using the *vif* function in the package *car* (Fox and Weisberg, 2011). VIFs for all models were below 3, indicating that there was no issue with multicollinearity (Zuur et al., 2009). To account for repeated measures, pride and lion ID were included as random effects in all models.

We used an information-theoretic approach to identify which factors explained the variation in the strength of greetings in different time periods (Burnham and Anderson, 2002). Due to the small sample sizes in this study, second order Akaike’s Information Criterion values (AICc) were calculated for each model. We also computed the difference between the best model and all other models (ΔAICc), including intercept only models, which enabled the most parsimonious model to be identified (Burnham and Anderson, 2002) (Tables 1 and 2). We used the Wald Chi-Square test in the R package *car* to determine the significance of the effect of fixed factors and interactions in final models, and the package *lsmeans* (Lenth, 2016) to report least square means and 95% confidence intervals (CIs) for single model factors. However, if more than one model had a ΔAICc < 2 we calculated model averaged parameters using the *MuMIn* package (Barton, 2016). Finally, the package *igraph* (Csardi and Nepusz, 2006) was used to create sociograms.

1. Results
   1. Female greetings over cub introductions

Networks in the periods prior to cubs being born were characterised by denser connections between females, compared to situations with cubs (Figures 1a-d). Whether a female was a mother or not was not included in the model for initiated greetings, but strength values decreased significantly between the pre- (least squares means [95% CIs] 15.3 [7.67-22.93]) and post-cub (5.63 [-1.99-13.26]) *χ*21 = 210.03, p < 0.001) periods (Table 3).

The strength of received greeting networks also decreased significantly in the post-cub periods (β = -0.8478, SE = 0.1292, *z* = 6.413, p *<* 0.001), and although mothers received fewer greetings than non-mothers, this was not significant (β = -0.1544, SE = 0.1953, *z* = 0.775, p = 0.43). The interaction between phase and motherhood was also not significant (β = 0.0790, SE = 0.1650, *z* = 0.470, p = 0.63).

3.1.1 Initiated greetings over sub-adulthood

Strength values tended to be higher for initiated greeting networks in sub-adult phases compared to the cub period (Table 4) (see Table 5 for means and CIs for all phases, *χ*210 = 68.254, p < 0.001). Amongst the age classes, cubs initiated the most and adults the fewest (cubs = 21.41 [9.2-33.61], sub-adults = 15.55 [4.17-26.93], adults = 10.58 [-0.83-22] *χ*22 = 33.484, p *<* 0.001). Overall, males initiated fewer greetings than females (males = 14.23 [2.24-26.31], females = 17.42 [5.67-29.16] *χ*21 = 15.832, p *<* 0.001). However the difference between the sexes might only apply to adults as the interaction between age and sex demonstrated that adult males initiated significantly fewer interactions than younger males (*χ*22 = 19.835, p *<* 0.001) (Figure 2).

3.1.2 Adult to offspring greetings

Adult males initiated fewer greetings towards younger individuals than females did (males = 6.94 [-8.58-22.46], females = 14.52 [1.01-28.03=] *χ*21 = 11.53, p < 0.001), but overall frequency of initiated interactions from adults towards offspring increased as they matured (see Table 5 for means and CIs for all phases, *χ*210 = 156.03, p < 0.001). Adult males also initiated fewer greetings towards female offspring than mature females did (males = 3.48 [-12.24-19.19], females = 10.93 [-2.39-24.25] *χ*21 = 9.28, p = 0.002). However, again, frequency of greetings from adults towards young females increased over sub-adulthood (see Table 5 for means and CIs for all phases, *χ*210 = 94.08, p < 0.001), particularly from an average age of 27-29 months and onwards. Young males similarly received more greetings from adults from 27-29 months (see Table 5 for means and CIs for all phases, *χ*210 = 96.587, p *<* 0.001). Although unlike female offspring, the sex of the adult did not influence the frequency of interactions towards young males.

3.1.3 Sub-adult to adult interactions

We observed the opposite effect with interactions from younger lions, and the frequency of greetings from sub-adults towards adults decreased as they matured. Four phases in particular showed significant decreases in greetings initiated by sub-adults (average age 30-32 months, β = -0.1733, SE = 0.069, *z* = 2.44, p = 0.014; 33-35 months, β = -0.247, SE = 0.063, *z* = 3.84, p *<* 0.001; 36-38 months, β = -0.1925, SE = 0.063, *z* = 2.99, p *=* 0.002; 39-41 months, β = -0.2449, SE = 0.063, *z* = 3.81, p *<* 0.001). There were only two phases (18-21 months, β = 0.029, SE = 0.069, *z* = 0.404, p = 0.68; 30-33 months, β = 0.076, SE = 0.069, *z* =1.077, p = 0.28) when sub-adults increased the frequency of interactions towards adults, but neither increase was significant. Between the sexes, sub-adult males initiated more adult-directed greetings than females did but this was also not significant (β = 0.035, SE = 0.0809, *z* = 0.430, p = 0.66).

Sub-adults of both sexes reduced their greetings significantly towards adult females (see Table 5 for means and CIs for all phases, *χ*210 = 56.52, p < 0.001) compared to cub phases, but the decrease towards males was not significant (β = -0.16022, SE = 0.092, *z* = 1.72, p = 0.084). Sub-adult males initiated more greetings than sub-adult females on mature males (β = 0.339, SE = 0.199, *z* = 1.684, p = 0.35), and sub-adult males also initiated fewer greetings than male cubs did on adult males (β = -0.06812, SE = 0.13148, *z* = 0.515, p = 0.60). However, none of the changes observed in greetings from sub-adult males towards adult males were significant.

3.1.4 Received greetings over sub-adulthood

Among the three age classes cubs (β = -0.396, SE = 0.075, *z* = 5.233, p < 0.001) and sub-adults (β = -0.242, SE = 0.095, *z* = 2.528, p =0.011) received fewer interactions than adults did (Table 6). When sub-adult phases were compared to the cub phase (Figures 3a and 3b), the phase representing an average sub-adult age range of 30-33 months (Figures 4a and 4b) showed a significant reduction in the strength of received interactions (β = -0.209, SE = 0.06, *z* = 3.469, p *<* 0.001). Two latter phases had large increases of received greetings over the cub period (average sub-adult age range 36-38 months: β = 0.124, SE = 0.053, *z* = 2.33, p =0.019; 42-44 months: β = 0.104, SE = 0.053, *z* = 1.964, p = 0.049). Finally, male cubs (β = -0.0536, SE = 0.08655, *z* = 0.618, p = 0.53) and sub-adults (β = -0.1019, SE = 0.14442, *z* = 0.704, p = 0.48) received fewer greetings than females of the same age classes, but the interaction between age and sex was not significant.

3.1.5 Betweenness centrality

For individual betweenness values (see Supplementary data), the null model was amongst the best models for both the analyses of adult female greetings and interactions over phases of sub-adulthood.

1. Discussion

In the present study we describe networks of greeting interactions in captive-bred lions over periods of change to group size, and the maturing of sub-adults. We found that as cubs are integrated into prides, both mothers and mothers without young decrease the strength of greetings networks towards one another. Our results also demonstrated that sub-adults the reduced frequency of adult-directed greetings as they matured, whereas adults increased the frequency of greetings towards offspring.

The mother-offspring relationship is one of the most intense relationships in mammals (Dunbar and Shultz, 2010). The development of this relationship between female vervet monkeys (*Chlorocebus aethiops*) and their offspring was observed to have a negative effect on the strength of grooming networks with wider group members (Borgeaud et al., 2017). The development of mother-cub relationships could partially account for the decrease of strength in greeting networks in our study. However, our results did not support the prediction that mothers’ interactions would decrease more than those of females without cubs. This suggests that the number of available social partners influenced all females’ interactions, regardless of an individual’s connection to the cubs. Although an increase in the number of social partners can negatively impact group cohesion, Ilany et al., (2015) showed that spotted hyena maintain their strongest social ties across years irrespective of environmental and demographic fluctuations. As captive animals do not need to perform a number of behaviours that their wild counterparts do (*e.g.* territorial defence, foraging, travelling) they are able to dedicate more time to social interactions (Matoba et al., 2013). This may be especially true for the pre-cub period when the lions would not have engaged in activities related to cub-rearing. Alternatively, they are not exposed to experiences that may create conditions when cohesion needs to be reinforced. For instance, females of the same pride will cooperate in contests with unfamiliar females (McComb et al., 1993; McComb et al., 1994). Following territorial encounters with rival groups, female blue monkeys engage in intense allogrooming with group mates (Cords, 2002). Whether the absence of cooperative activities within the study prides affected the strength of their interactions is unknown. However, if individuals from these prides are intended for reintroduction, determining their ability to maintain cohesion during contests with competitors would prove a worthwhile avenue for future study.

Despite a lack of dispersal in these prides, greeting networks increased in strength over sub-adulthood. Further, greetings became more balanced between the age classes as offspring matured. Smith et al., (2013) also found that affiliative interactions become increasingly symmetric across ontogeny between yellow-bellied marmot (*Marmota flaviventris*) mothers and their offspring. Like lions, marmots have a male-biased dispersal system and around 50% of female yearlings also disperse (Armitage, 1991; Van Vuren & Armitage, 1994). Although our study was not solely focussed on mother-offspring interactions, like Smith et al., (2013) our results are consistent with offspring becoming less dependent on adults are they mature. We also identified an average age of 27-30 months when increases in greetings from adults began. Why this stage in sub-adulthood marks a change in behaviour from adults may be due to a change in the sub-adults’ social value. The value of a social partner may be reflected in the amount of affiliative behaviour directed towards them. Dominant male meerkats for example groom subordinate males, who help defend the group, for longer than they groom subordinate females (Kutsukake and Clutton-Brock, 2010). Heinsohn et al., (1996) studied the development of cooperation in territorial behaviour in juvenile lions (8-42 months). They found that when juveniles under 18-months were unaccompanied by adults, they never approached intruders. However, by 37-42 months of age, unaccompanied juveniles had more than a 70% likelihood of challenging intruders. As larger prides and coalitions are more successful in contests with rivals, sub-adults that are take an effective role in defending the pride should make more valuable social partners (Packer et al., 1988; Mosser and Packer, 2009).

Contrary to our prediction, sub-adults of both sexes received more greetings from adults. For sub-adult females, the increase of greetings from adult females suggests that these prides are within optimal limits, although dispersal of female lions is more common when group size and food abundance interact (VanderWaal et al., 2009). Therefore, it is likely that the provision of food to these prides removed a significant source of competition and by extension any pressure for females to disperse. However, we had expected mature females to decrease the frequency of interactions with maturing males but this was not the case. If sub-adult males are able to remain in their natal pride until at least 37 months before dispersing they have a high probability of survival (Elliot et al., 2014). As growth in mass is most linear in lions up until 36 months, males who disperse at younger ages are likely at a competitive disadvantage (Smuts et al., 1980; Elliot et al., 2014). Competitive ability has been linked to the onset of natal dispersal in species like Belding’s ground squirrels (*Spermophilus beldingi*) and Eurasian beavers (*Castor fiber*) (Holekamp, 1986; Mayer et al., 2017). Our results indicate that if sub-adults are not evicted by the primary dispersal trigger (incoming males) then females may tolerate their maturing sons remaining in the natal pride to improve their chances of successful dispersal (Ekman et al., 2001; Mayer et al., 2017).

Increases of interactions between males appear to provide some support for our prediction that lone mature males would recruit their sons into a coalition. However males greet other males more often than females, and to have confidence in the previous statement a range of coalition sizes would need to be tested (Matoba et al., 2013). Additionally, any competition that could have arisen between fathers and sons for mates due to the sub-adults being unable to disperse was removed by the use of contraceptive implants on female pride members. With seven females in the Ngamo pride and eight in the Dambwa pride able to reproduce and no emigration occurring, a lack of contraception would lead to a rapid increase in pride size, which could have also increased the frequency of competitive interactions within prides. Therefore, how our results compare to natural populations and the function of a dynamic network in lion prides requires further investigation.

5. Conclusion

In conclusion, our study demonstrates that lions vary social interaction patterns in response to changes in group size and changing demographics. Additionally, our results highlighted that as younger pride members mature, greetings become increasingly balanced between the age classes: changes that coincide with dispersal ages and competitive ability. We therefore suggest that affiliative interactions between lions may assist in the recruitment and dispersal of sub-adults in lion prides

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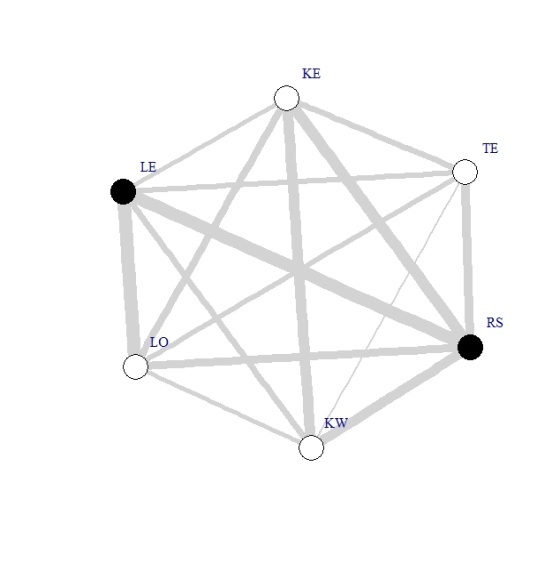
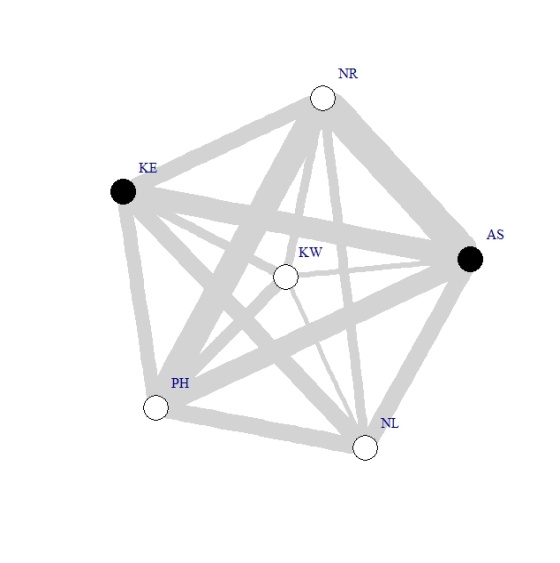
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Table 1: Competing models for LMMs of network metrics over cub introduction phases between females (1a-c) and sub-adult phases (2a-c). Bold indicates best model/s as determined by ΔAICc values.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Models | Df | LogLik | AICc | ΔAICc | Weight |
| 1a) Initiated greetings: females  **Age \* Sex + Phase (full model)** | **19** | **-643.478** | **1329.1** | **0.00** | **0.985** |
| Age + Sex + Phase | 17 | -650.184 | 1337.6 | 8.58 | 0.014 |
| Age + Phase | 16 | -653.602 | 1342.1 | 13.03 | 0.001 |
| Sex + Phase | 15 | -660.035 | 1352.6 | 23.55 | 0.000 |
| Phase | 14 | -661.313 | 1352.8 | 23.77 | 0.000 |
| Age \* Sex | 9 | -672.629 | 1364.2 | 35.12 | 0.000 |
| Age + Sex | 7 | -679.627 | 1373.8 | 44.76 | 0.000 |
| Age | 6 | -682.589 | 1377.6 | 48.54 | 0.000 |
| Sex | 5 | -684.141 | 1378.6 | 46.52 | 0.000 |
| Intercept (only) | 4 | -685.411 | 1379.0 | 49.96 | 0.00 |
| 1b) Received greetings: adult females  **Age + Sex + Phase** | **17** | **-642.762** | **1322.8** | **0.00** | **0.407** |
| **Age \* Sex + Phase (full model)** | **19** | **-640.367** | **1322.9** | **0.05** | **0.398** |
| **Age + Phase** | **16** | **-644.687** | **1324.3** | **1.47** | **0.195** |
| Phase | 14 | -657.430 | 1376.3 | 22.28 | 0.000 |
| Sex + Phase | 15 | -657.254 | 1347.0 | 24.25 | 0.000 |
| Age \* Sex | 9 | -644.775 | 1350.5 | 27.68 | 0.000 |
| Age + Sex | 7 | -688.202 | 1351.0 | 28.18 | 0.000 |
| Age | 6 | -670.085 | 1352.6 | 29.80 | 0.000 |
| Intercept (only) | 4 | -684.072 | 1376.3 | 53.55 | 0.000 |
| Sex | 5 | -683.891 | 1376.3 | 53.55 | 0.000 |
| 1c) Betweenness: Adult Females |  |  |  |  |  |
| **Intercept (only)**  **Age** | **4**  **6** | **-637.447**  **-630.464** | **1273.1**  **1273.4** | **0.00**  **0.26** | **0.335**  **0.295** |
| Age + Sex | 7 | -630.278 | 1275.1 | 2.03 | 0.121 |
| Sex | 5 | -632.424 | 1275.1 | 2.06 | 0.120 |
| Age + Phase | 16 | -621.162 | 1277.2 | 4.12 | 0.043 |
| Age \* Sex | 9 | -629.175 | 1277.3 | 4.18 | 0.041 |
| Age + Sex + Phase | 17 | -620.894 | 1279.1 | 5.97 | 0.017 |
| Phase | 14 | -624.442 | 1279.1 | 6.00 | 0.017 |
| Age \* Sex + Phase (full model) | 19 | -619.580 | 1281.3 | 8.17 | 0.006 |
| Sex + Phase | 15 | -624.415 | 1281.4 | 8.28 | 0.005 |
| 2a) Initiated greetings: sub-adult phases |  |  |  |  |  |
| **Age \* Sex + Phase (full model)** | **19** | **-643.478** | **1329.1** | **0.00** | **0.985** |
| Age + Sex + Phase | 17 | -650.184 | 1337.6 | 8.58 | 0.014 |
| Age + Phase | 16 | -653.602 | 1342.1 | 13.03 | 0.001 |
| Sex + Phase | 15 | -660.035 | 1352.6 | 23.55 | 0.000 |
| Phase | 14 | -661.313 | 1352.8 | 23.77 | 0.000 |
| Age \* Sex | 9 | -672.629 | 1364.2 | 35.12 | 0.000 |
| Age + Sex | 7 | -679.627 | 1373.8 | 44.76 | 0.000 |
| Age | 6 | -682.589 | 1377.6 | 48.54 | 0.000 |
| Sex | 5 | -684.141 | 1378.6 | 46.52 | 0.000 |
| Intercept (only) | 4 | -685.411 | 1379.0 | 49.96 | 0.00 |
| 2b) Received greetings: sub-adult phases |  |  |  |  |  |
| **Age + Sex + Phase** | **17** | **-642.762** | **1322.8** | **0.00** | **0.407** |
| **Age \* Sex + Phase (full model)** | **19** | **-640.367** | **1322.9** | **0.05** | **0.398** |
| **Age + Phase** | **16** | **-644.687** | **1324.3** | **1.47** | **0.195** |
| Phase | 14 | -657.430 | 1376.3 | 22.28 | 0.000 |
| Sex + Phase | 15 | -657.254 | 1347.0 | 24.25 | 0.000 |
| Age \* Sex | 9 | -644.775 | 1350.5 | 27.68 | 0.000 |
| Age + Sex | 7 | -688.202 | 1351.0 | 28.18 | 0.000 |
| Age | 6 | -670.085 | 1352.6 | 29.80 | 0.000 |
| Intercept (only) | 4 | -684.072 | 1376.3 | 53.55 | 0.000 |
| Sex | 5 | -683.891 | 1376.3 | 53.55 | 0.000 |
| 2c) Betweenness: Sub-adult phases |  |  |  |  |  |
| **Intercept (only)** | **4** | **-637.447** | **1273.1** | **0.00** | **0.335** |
| **Age** | **6** | **-630.464** | **1273.4** | **0.26** | **0.295** |
| Age + Sex | 7 | -630.278 | 1275.1 | 2.03 | 0.121 |
| Sex | 5 | -632.424 | 1275.1 | 2.06 | 0.120 |
| Age + Phase | 16 | -621.162 | 1277.2 | 4.12 | 0.043 |
| Age \* Sex | 9 | -629.175 | 1277.3 | 4.18 | 0.041 |
| Age + Sex + Phase | 17 | -620.894 | 1279.1 | 5.97 | 0.017 |
| Phase | 14 | -624.442 | 1279.1 | 6.00 | 0.017 |
| Age \* Sex + Phase (full model) | 19 | -619.580 | 1281.3 | 8.17 | 0.006 |
| Sex + Phase | 15 | -624.415 | 1281.4 | 8.28 | 0.005 |

Table 2: Competing models for LMMs of greetings from adults to sub-adults, and sub-adults to adults. Bold indicates best model which was determined on ΔAICc values.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | Df | LogLik | AICc | ΔAICc | Weight |
| 1a) Adults to offspring  **Phase + Sex** | **15** | **-350.996** | **737.2** | **0.00** | **0.903** |
| Phase | 14 | -354.585 | 741.7 | 4.48 | 0.096 |
| Phase \* Sex (full model) | 25 | -343.004 | 751.9 | 14.65 | 0.001 |
| Sex | 5 | -397.739 | 806.1 | 68.86 | 0.000 |
| Intercept (only) | 4 | -401.563 | 811.5 | 74.30 | 0.000 |
| 1b) Adults to female offspring  **Phase + Sex** | **15** | **-342.243** | **719.7** | **0.00** | **0.858** |
| Phase | 14 | -345.401 | 723.3 | 3.61 | 0.141 |
| Phase \* Sex (full model) | 25 | -333.866 | 733.6 | 13.88 | 0.001 |
| Sex | 5 | -375.248 | 761.1 | 41.38 | 0.000 |
| Intercept (only) | 4 | -378.498 | 761.4 | 45.68 | 0.000 |
| 1c) Adults to male offspring  **Phase** | **14** | **-247.938** | **528.4** | **0.00** | **0.762** |
| Phase + Sex | 15 | -237.934 | 531.1 | 2.70 | 0.198 |
| Phase \* Sex (full model) | 25 | -234.211 | 534.3 | 5.89 | 0.040 |
| Intercept (only) | 4 | -281.906 | 572.2 | 43.82 | 0.000 |
| Sex | 5 | -281.906 | 574.4 | 46.02 | 0.000 |
| 2a) Offspring to adults |  |  |  |  |  |
| **Phase** | **14** | **-381.345** | **795.8** | **0.00** | **0.530** |
| **Phase + Sex** | **15** | **-380.819** | **797.6** | **1.75** | **0.221** |
| Age + Phase | 15 | -381.266 | 798.5 | 2.65 | 0.141 |
| Age + Phase + Sex | 16 | -380.712 | 800.2 | 4.41 | 0.058 |
| Age \* Sex + Phase (full model) | 17 | -379.404 | 800.6 | 4.74 | 0.049 |
| Age | 5 | -399.871 | 810.4 | 14.59 | 0.000 |
| Intercept (only) | 4 | -401.631 | 811.7 | 15.88 | 0.000 |
| Age + Sex | 6 | -399.427 | 811.8 | 15.98 | 0.000 |
| Sex | 5 | -401.112 | 812.9 | 17.07 | 0.000 |
| Age \* Sex | 7 | -399/051 | 813.4 | 17.55 | 0.000 |
| 2b) Offspring to adult females |  |  |  |  |  |
| **Phase** | **14** | **-363.182** | **759.5** | **0.00** | **0.614** |
| Phase + Sex | 15 | -363.072 | 762.1 | 2.58 | 0.169 |
| Age + Phase | 15 | -363.140 | 762.2 | 2.72 | 0.158 |
| Age + Phase + Sex | 16 | -363.039 | 764.9 | 5.39 | 0.041 |
| Age \* Sex + Phase (full model) | 17 | -362.366 | 766.5 | 6.99 | 0.019 |
| Intercept (only) | 4 | -384.760 | 778.0 | 18.47 | 0.000 |
| Age | 5 | -383.939 | 778.5 | 19.05 | 0.000 |
| Sex | 5 | -384.649 | 780.0 | 20.47 | 0.000 |
| Age + Sex | 6 | -383.856 | 780.6 | 21.16 | 0.000 |
| Age \* Sex | 7 | -383.766 | 782.8 | 23.30 | 0.000 |
| 2c) Offspring to adult males |  |  |  |  |  |
| **Age** | **5** | **-292.583** | **595.8** | **0.00** | **0.304** |
| **Age + Sex** | **6** | **-291.602** | **596.1** | **0.31** | **0.260** |
| **Age \* Sex** | **7** | **290.487** | **596.2** | **0.41** | **0.248** |
| Sex | 5 | -294.447 | 599.6 | 3.73 | 0.047 |
| Intercept (only) | 4 | -295.590 | 599.6 | 3.79 | 0.046 |
| Phase | 14 | -283.959 | 601.0 | 5.21 | 0.022 |
| Age + Phase | 15 | -282.729 | 601.4 | 5.56 | 0.019 |
| Age + Phase + Sex | 16 | -281.343 | 601.5 | 5.66 | 0.018 |
| Phase + Sex | 15 | -282.781 | 601.5 | 5.66 | 0.018 |
| Age \* Sex + Phase | 17 | -279.894 | 601.5 | 5.71 | 0.018 |

1a 1b 

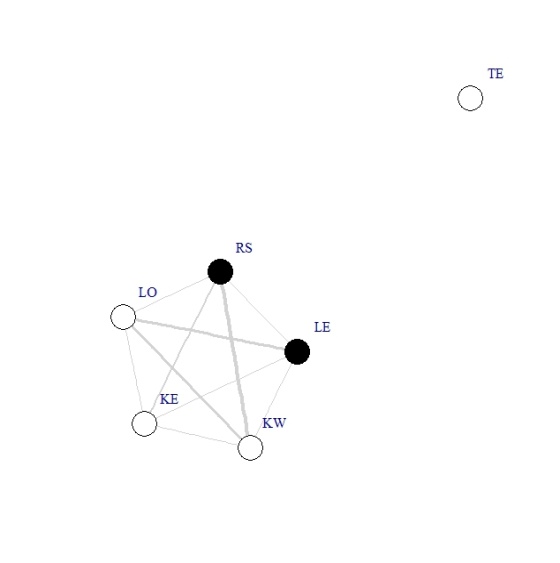
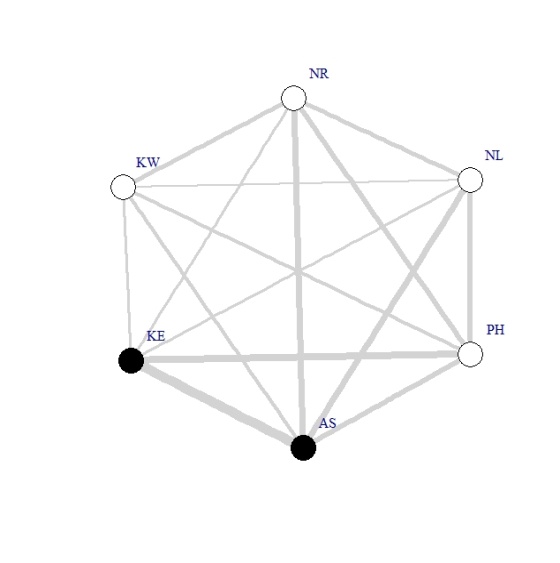
1c 1d 

Figure 1a: Pre-cub Dambwa and Figure 1b: post-cub Dambwa pride adult female greeting interaction networks. Figure 1c: Pre-cub Dambwa and Figure 1d: post cub Ngamo pride adult female greeting interaction networks. Black nodes indicate mothers (or future mothers), white nodes are non-mothers.

Table 3: Social network strength of initiated and received greetings of adult lionesses before and after cubs.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Pride | ID | Pre-cubs  Initiated | Pre-cubs Received | Post-cubs Initiated | Post-cubs Received |
| D | KE | 13.6 | 11.62 | 3.64 | 3.0 |
| D | KW | 8.72 | 13.6 | 4.24 | 4.24 |
| D | LE\* | 14.14 | 13.42 | 3.87 | 2.0 |
| D | LO | 12.65 | 13.0 | 2.83 | 2.83 |
| D | RS\* | 15.33 | 15.49 | 3.46 | 5.66 |
| D | TE | 12.0 | 9.38 | - | - |
| N | AS\* | 18.84 | 21.45 | 8.94 | 12.65 |
| N | KE\* | 18.84 | 20.37 | 9.38 | 6.63 |
| N | KW | 11.62 | 14.32 | 5.74 | 8.06 |
| N | NL | 19.1 | 13.0 | 10.72 | 4.47 |
| N | NR | 22.69 | 15.33 | 10.49 | 5.2 |
| N | PH | 16.28 | 22.47 | 4.9 | 12.25 |

\* denotes mother within a pride. Pride D = Dambwa, N = Ngamo.

Table 4: Social network strength of initiated interactions over sub-adult phases: Bold numbers denote the highest within pride value for that phase

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Phase (average age of sub-adults in months) | | | | | | | | | | |
| Pride | ID | 15- 18 m | 18-21 m | 21-24 m | 24-27m | 27-30 m | 30-33 m | 33-36 m | 36-39 m | 39-42 m | 42-45 m | 45-48 m |
| D | KE1 | 6.9 | 7.8 | 10.9 | 13.8 | 8.1 | 5 | 14.1 | - | - | - | - |
| D | KW1 | 7.1 | 4 | 12.3 | 13.2 | 6.3 | 8.7 | 13.2 | - | - | - | - |
| D | LE1\* | 7.3 | 4.2 | 16.7 | 14.1 | 2.5 | 2.5 | **18.4** | - | - | - | - |
| D | LO1 | 4.9 | 1.4 | 11.5 | 13.8 | 4.6 | 7.4 | 17.6 | - | - | - | - |
| D | RS1\* | 8.8 | 7.4 | 16.2 | 13.4 | **10.6** | 7.8 | 8.5 | - | - | - | - |
| D | ZU1 | 2.5 | 0 | 4 | 1 | 6.3 | 6.9 | 9.4 | - | - | - | - |
| D | RS12 | 11.7 | 7.8 | 9.2 | 14.4 | **10.6** | 4.5 | 4.9 | - | - | - | - |
| D | RS22 | 8.4 | 4 | 11.3 | 10.9 | 5.7 | 3 | 7.4 | - | - | - | - |
| D | RS32 | 14.1 | 10.9 | 14.1 | 14.1 | 6.3 | 8.8 | 8.4 | - | - | - | - |
| D | LE12 | 18.3 | 6.7 | 17.2 | 18 | 5.5 | **12.3** | 15.3 | - | - | - | - |
| D | LE22 | **18.4** | 10.2 | **20.5** | 17.9 | 9.9 | 9.4 | 14.1 | - | - | - | - |
| D | LE32 | 13.6 | **12.7** | 17.6 | **18.4** | 5.5 | 3 | 14.1 | - | - | - | - |
| N | AS1\* | 18.7 | 26.1 | 11.6 | 19.6 | 23 | 25.1 | 4.6 | 22.1 | 25.7 | 23.9 | 24.1 |
| N | KE1\* | 12.3 | 24.7 | 14 | 21.7 | 20.6 | 28.6 | 3.9 | 22.4 | 25.3 | 24.7 | **28.3** |
| N | KW1 | 6.7 | 23.7 | 18.5 | 20.9 | 18.7 | 29.2 | 3.6 | **26.5** | **28.1** | **26.5** | 27.6 |
| N | NL1 | 8.8 | 15.9 | 14.1 | 19.8 | 21.8 | 28.1 | 3.9 | 22.9 | 27 | 23.7 | 22.5 |
| N | PH1 | 2.8 | 16.7 | 13.9 | 21.2 | 16.9 | 27 | 5 | 22.4 | 24.1 | 23 | 22.6 |
| N | MI1 | 2 | 3.9 | 1 | 10.6 | 3 | 6.7 | 4.9 | 7.4 | 17.9 | 7.2 | 8.1 |
| N | AT12 | 17.2 | 28.6 | **25.5** | 27.8 | 27 | 31.8 | 4.2 | 16.7 | 20.7 | 19.4 | 23 |
| N | KE32 | 14.7 | 27.4 | 15.5 | 22.1 | 25.7 | 33.3 | **5.4** | 21.2 | 21.7 | 17.5 | 22.7 |
| N | KE42 | 14.7 | 21.8 | 17.4 | 20.6 | 22.6 | 22.1 | 4.8 | 16.4 | 12.7 | 13.6 | 22.7 |
| N | AS42 | 23.7 | 28.9 | 22 | **28.1** | **30.2** | **34.5** | 4.1 | 19.8 | 27 | 23 | 26.5 |
| N | AS52 | **26.7** | **29.1** | 22.4 | 23.8 | 22.9 | 34.2 | 3.5 | 24.1 | 24.6 | 21.2 | 20.1 |

\* indicates mothers of sub-adults. Pride D = Dambwa, N = Ngamo.

1 after a lion’s ID indicates an adult pride member, whereas a 2 signals a cub/sub-adult.

Table 5: Least squares means and 95% confidence intervals for initiated greetings over phases of sub-adulthood.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Model |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Initiated greeting patterns: sub-adulthood | | | Adult initiated greetings to offspring | | | Adult initiated greetings to female offspring | | | Adult initiated greetings to male offspring | | | Offspring initiated greetings to adults | | |
| Phase | Mean | Lower CI | Upper CI | Mean | Lower CI | Upper CI | Mean | Lower CI | Upper CI | Mean | Lower CI | Upper CI | Mean | Lower CI | Upper CI |
| 15-18 m | 10.39 | -0.09 | 20.88 | -0.69 | -11.63 | 10.24 | -1.23 | -12.18 | 9.71 | 0.58 | -0.85 | 2.02 | 23.88 | -18.76 | 66.52 |
| 18-21 m | 13.65 | 3.22 | 24.08 | 2.56 | -8.38 | 13.49 | 1.43 | -9.51 | 12.38 | 1.17 | -0.27 | 2.6 | 24.88 | -17.76 | 67.52 |
| 21-24 m | 14.23 | 3.8 | 24.67 | 2.56 | -8.38 | 13.49 | 1.68 | -9.26 | 12.63 | 1.42 | -0.02 | 2.85 | 20.43 | -22.21 | 63.07 |
| 24-27 m | 18.66 | 8.12 | 29.2 | 4.64 | -6.29 | 15.57 | 3.27 | -7.68 | 14.21 | 1.42 | -0.02 | 2.85 | 26.61 | -16.03 | 69.25 |
| 27-30 m | 14.97 | 4.43 | 25.5 | 4.47 | -6.46 | 15.41 | 3.02 | -7.93 | 13.96 | 1.5 | 0.06 | 2.92 | 21.43 | -21.21 | 64.07 |
| 30-33 m | 17.81 | 7.27 | 28.35 | 12.89 | 1.96 | 23.82 | 9.27 | -1.68 | 20.21 | 3.67 | 2.23 | 5.1 | 32.52 | -10.12 | 75.16 |
| 33-36 m | 9.71 | -0.08 | 20.25 | 11.14 | 0.21 | 22.1 | 7.1 | -3.84 | 18.04 | 4.08 | 2.65 | 5.52 | 16.97 | -25.67 | 59.61 |
| 36-39 m | 17.32 | 5.94 | 28.7 | 17.95 | 5.76 | 30.15 | 13.01 | 0.98 | 25.04 | 4.93 | 2.95 | 6.9 | 6.44 | -38.02 | 50.89 |
| 39-42 m | 20.32 | 8.94 | 31.7 | 25.28 | 13.09 | 37.48 | 16.84 | 4.81 | 28.87 | 8.43 | 6.45 | 10.4 | 6.44 | -38.02 | 50.89 |
| 42-45 m | 17.49 | 6.12 | 28.87 | 17.28 | 5.09 | 29.48 | 10.84 | -1.19 | 22.87 | 6.43 | 4.45 | 8.4 | 6.84 | -37.62 | 51.29 |
| 45-48 m | 19.77 | 8.39 | 31.15 | 19.95 | 7.76 | 32.15 | 14.01 | 1.98 | 26.04 | 5.93 | 3.95 | 7.9 | 14.64 | -29.82 | 59.09 |

Figure 2: Mean ± SE bars initiated greeting interactions over sub-adulthood phases. A significant interaction between age and sex was observed, as adult males initiated fewer greetings than males of younger age classes.

Table 6: Social network strength of received interactions over sub-adult phases: Bold numbers denote the highest within pride value for that phase

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Phase (average age of sub-adults in months) | | | | | | | | | | |
| Pride | ID | 15-18 m | 18-21 m | 21-24 m | 24-27 m | 27-30 m | 30-33 m | 33-36 m | 36-39 m | 39-42 m | 42-45 m | 45-48 m |
| D | KE1 | 10.6 | 6.7 | 8.5 | 13.4 | 4.9 | 6.3 | 10.6 | - | - | - | - |
| D | KW1 | 10.9 | 4.9 | 13.4 | 14.1 | 9.9 | 3 | 9.5 | - | - | - | - |
| D | LE1\* | 16.4 | 7.8 | 19.8 | 21.2 | 9.2 | 9.4 | 12.4 | - | - | - | - |
| D | LO1 | 10.2 | 5.9 | 13.8 | 14.1 | 6.9 | 6.9 | 12.7 | - | - | - | - |
| D | RS1\* | 14.4 | 8.7 | 17.6 | 15.6 | 7.4 | 7.4 | 14.1 | - | - | - | - |
| D | ZU1 | **30.6** | **19.5** | **30.8** | **28.5** | **15.9** | **15.5** | **22.1** | - | - | - | - |
| D | RS12 | 4.5 | 4 | 9.9 | 8.4 | 4.5 | 6.5 | 8.1 | - | - | - | - |
| D | RS22 | 6.3 | 4.5 | 15.5 | 14.1 | 8.8 | 10.6 | 16.4 | - | - | - | - |
| D | RS32 | 6.3 | 2.9 | 9.9 | 12.7 | 3.5 | 3.5 | 11.6 | - | - | - | - |
| D | LE12 | 3.9 | 2.5 | 8.8 | 6.5 | 4 | 3 | 7.8 | - | - | - | - |
| D | LE22 | 1 | 4.5 | 4.9 | 6.5 | 3 | 0 | 6.7 | - | - | - | - |
| D | LE32 | 3.2 | 4 | 4 | 4.2 | 3.5 | 7.4 | 13.1 | - | - | - | - |
|  |  |  |  |  |  |  |  |  |  |  |  |  |
| N | AS1\* | **28.1** | 31.9 | **27.2** | **32.4** | 29.4 | **41.5** | 3.4 | **26.3** | **30.2** | **28.1** | 28.8 |
| N | KE1\* | 19.7 | 27.2 | 19.2 | 27.6 | 23.6 | 26.5 | 3.9 | 20.3 | 19.8 | 20.9 | 24.3 |
| N | KW1 | 12.3 | 21.6 | 16.4 | 21.2 | 20.4 | 28.1 | 4.8 | 17.6 | 16.5 | 17.4 | 21.2 |
| N | NL1 | 8.5 | 16.9 | 10.6 | 13.2 | 15.8 | 19.9 | **5.8** | 15 | 19.9 | 17.8 | 15.6 |
| N | PH1 | 18.7 | 32.2 | 24.9 | 30.2 | 24.9 | 37.9 | 3.7 | 24 | 25.1 | 23.8 | **31.1** |
| N | MI1 | 24.6 | **36.5** | 23.8 | 24.9 | **31.8** | 30 | 3.7 | 18.9 | 27.5 | 20.6 | 25.5 |
| N | AT12 | 10.3 | 19.6 | 14 | 18 | 15.6 | 24.2 | 4.5 | 20 | 25.3 | 17.4 | 22.5 |
| N | KE32 | 5.9 | 11.6 | 9.2 | 16.4 | 21.9 | 23.8 | 4.3 | 20.1 | 24.7 | 21.6 | 19.6 |
| N | KE42 | 5.5 | 11.7 | 9.2 | 15.3 | 20.1 | 25.3 | 4.9 | 18.3 | 20.1 | 18.7 | 19.4 |
| N | AS42 | 3 | 14.4 | 9.5 | 21.2 | 13.6 | 18.3 | 5.2 | 22.7 | 21.2 | 18.5 | 21.2 |
| N | AS52 | 6.9 | 13.2 | 9.9 | 13.9 | 13.6 | 22.7 | 3.7 | 18.7 | 25.1 | 18.5 | 17.9 |

\* indicates mothers of sub-adults. Pride D = Dambwa, N = Ngamo. 1 after a lion’s ID indicates an adult pride member, whereas a 2 signals a cub/sub-adult.

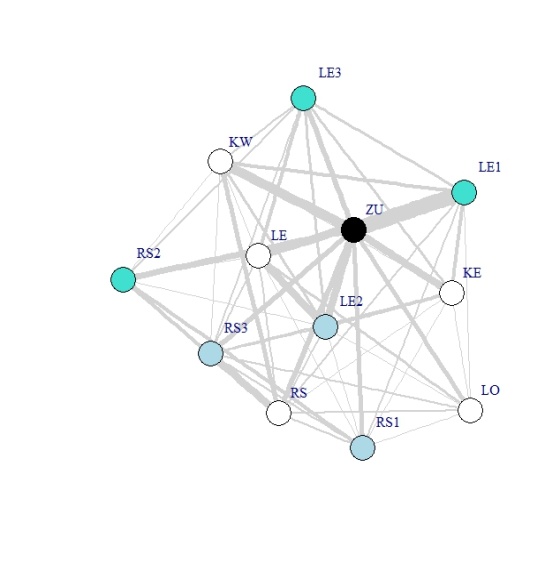
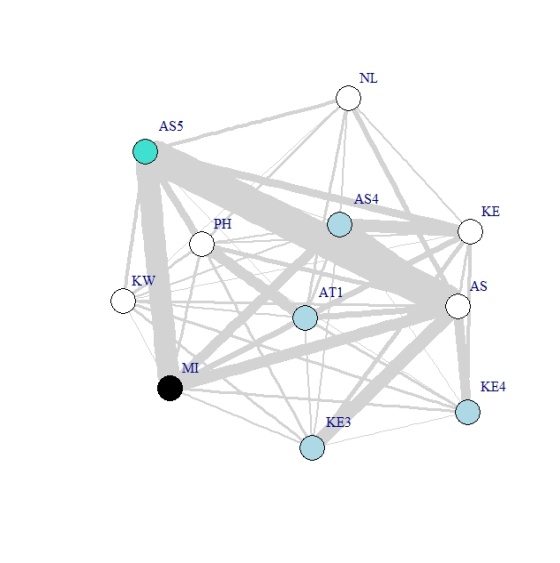
3a 3b 

Figure 3a: Dambwa and 3b: Ngamo greeting interaction networks, all offspring < 18 months. Black nodes = adult males, white nodes = adult females, pale blue nodes = female cubs and turquoise nodes = male cubs.

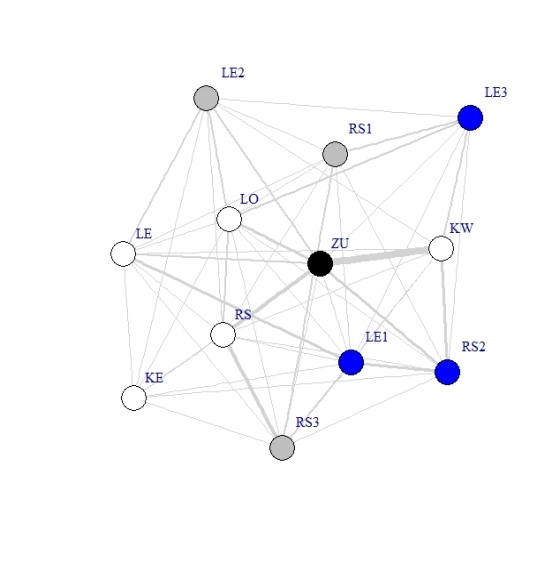
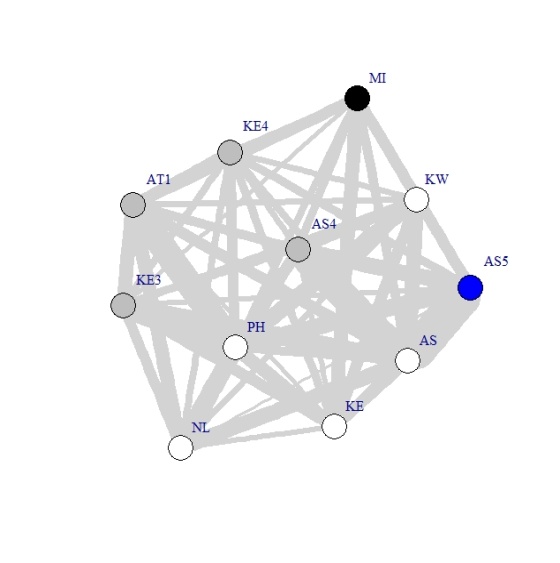
4a  4b 

Figure 4a: Dambwa and Figure 4b: Ngamo greeting interaction networks, average sub-adult age 30-33 months. Black nodes = adult males, white nodes = adult females, grey nodes = sub-adult females, dark blue nodes = sub-adult males.

1. The African Lion & Environmental Research Trust [↑](#footnote-ref-1)