

ORIGINAL ARTICLE

Inter-group associations in Mongolian gerbils: Quantitative evidence from social network analysis

Ke DENG, Wei LIU and Dehua WANG

State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, China and University of Chinese Academy of Sciences, Beijing, China

Abstract

Animals often interact non-randomly with conspecifics, and association preferences can differ across life-history stages to maximize individuals' fitness. Mongolian gerbils (*Meriones unguiculatus*) are a social rodent that live in highly seasonal habitats and display seasonal fluctuations in population density, growth rate and the size of overlapped home ranges. Nevertheless, whether gerbils modify their social relationships at different life-history stages remains unknown. Here, we used social network analysis to examine whether social associations differ between the sexes and between life-history stages in a wild population of Mongolian gerbils. We quantified social attributes at both group level (assortativity) and individual level (social differentiation and degree, closeness and betweenness centrality); these attributes reflect individuals' social preferences and their potential influence on others in the network. We found that both male and female gerbils established fewer inter-group social connections during the food-hoarding season than during the breeding season, revealing constraints on sociality. Similarly, during the food-hoarding season, degree centrality and social differentiation increased significantly whereas closeness and betweenness centrality decreased significantly. Together, these results suggest that gerbils have relatively more partners and preferred associations and decreased influence over others in the network during the food-hoarding season. In addition, we found no significant difference in any of the social attribute between males and females, but there was a significant interaction effect between sex and season on degree, closeness and betweenness centrality. Our results demonstrate that Mongolian gerbils adjust their association strategies to adapt to the changes of life history. Such adjustments may balance the costs/benefits associated with survival and reproduction.

Key words: centrality, inter-group associations, life history, *Meriones unguiculatus*, social network analysis

Correspondence: Wei Liu and Dehua Wang, Institute of Zoology, Chinese Academy of Sciences, Beichen Xilu, Chaoyang, Beijing 100101, China.
Email: liuwei@ioz.ac.cn; wangdh@ioz.ac.cn

INTRODUCTION

It is increasingly recognized that animals often interact non-randomly with group members (Kurvers *et al.* 2014). Association preferences based on sex, age and kinship have been observed in a wide diversity of organisms (Croft *et al.* 2005; Walker *et al.* 2008; Wey & Blumstein 2010; Hirsch 2011). However, ecological factors (e.g. food availability and climate) can af-

fect survival, reproduction or sex ratio, and, thus, drive variation in social groups and social systems (Bulter 1980; Crockett & Eisenberg 1987; Krebs 2015; Li *et al.* 2016). Such population-level effects may alter group size or group members and may create new opportunities for individuals to interact (Maldonado-Chaparro *et al.* 2015). Animals may alter behavioral strategies based on social background to maximize their fitness (Owen *et al.* 2017), therefore, association preferences can differ between ecological contexts (Kurvers *et al.* 2013). For instance, spotted hyenas (*Crocuta crocuta* Erxleben, 1777), animals with fission–fusion dynamics, make flexible decisions regarding which coalitions to join based on information about their immediate social and ecological contexts (Smith *et al.* 2010).

Moreover, animals can modify their social relationships to adapt to the temporal social environment (e.g. different season or life-history stages) (Krause & Ruxton 2002; Zhang *et al.* 2014; Owen *et al.* 2017). For example, barnacle geese (*Branta leucopsis* Bechstein, 1803) preferentially associate with familiar individuals when foraging but select unfamiliar partners during mate choice (Kurvers *et al.* 2013). Similarly, study of degus (*Octodon degus* Molina, 1782) has demonstrated that females have a larger number of preferred social partners than males during lactation, revealing that social relationships are particularly important for females during this period (Wey *et al.* 2013). For social animals, inter-group associations may produce benefits such as the maintenance of social rank (Arseneau-Robar *et al.* 2017) but may also impose potential costs for individuals (e.g. injuries or death; Mitani *et al.* 2010). However, there is a lack of knowledge about how social rodent species change association strategies in response to variation in life history.

Mongolian gerbils (*Meriones unguiculatus* Milne-Edwards, 1867) are social rodents that inhabit typical steppe, desert steppe and desert habitats in northern China, Mongolia and the Trans-Baikal area of Russia (Wilson & Reeder 2005). The reproduction and recruitment of Mongolian gerbils occur mainly from March to August (Liu *et al.* 2007, 2009), and they start to store food from September to October (Ågren *et al.* 1989a,b). Thus, there are 2 distinct life-history stages in Mongolian gerbils: the breeding season (March–August) and the food-hoarding season (September–October). Mongolian gerbils live in groups of 2 to 18 individuals year-round (Liu *et al.* 2009), and each social group occupies an exclusive burrow system (Ågren *et al.* 1989a). The home range size of a social group increases with the

number of male gerbils in the group during the breeding season, whereas it is positively correlated with the number of female group members during the food-hoarding season (Wang *et al.* 2011). In addition, home-range overlap is significantly higher during the breeding season compared to food-hoarding season (i.e. non-breeding season) (Wang *et al.* 2011). Within groups, male gerbils range more widely and are generally more active than female gerbils (Ågren *et al.* 1989a). These characteristics make Mongolian gerbils a good model species to investigate seasonal changes and sex differences in social associations, which have not been thoroughly examined in this species.

Here, we used social network analysis to quantify how individuals varied their social associations along with changes in social environment in a wild population of Mongolian gerbils. Social network analysis is a powerful method for investigating ecological and evolutionary processes in animal sociality (Krause *et al.* 2009; Kurvers *et al.* 2014; Pinter-Wollman *et al.* 2014). This method provides a suite of measures that allowed us to statistically analyze social structure, direct as well as indirect relationships between individuals, and the role of an individual in social networks (Wey *et al.* 2008; Makagon *et al.* 2012). We focused on a group-level (assortativity) and 4 individual-level (social differentiation, degree, closeness and betweenness) social attributes that permitted us to understand the variation in social structure and to evaluate how extensively individuals were involved in relationships with others.

We assumed that seasonal life-history traits would drive variation in social associations. Because Mongolian gerbils reduce overlap of home ranges during the food-hoarding season (Wang *et al.* 2011), we predicted that there are more associations between inter-group members during the breeding season than during the food-hoarding season. We then hypothesized that both sex and season affect individuals' social network positions. Because Mongolian gerbils are engaged in storing food during the non-breeding season, we predicted that individuals reduce their number of social partners and that network connectedness is decreased. We also predicted that male gerbils have greater influence over others compared to females, because males of this species usually dominate females (Ågren *et al.* 1989a).

MATERIALS AND METHODS

Field data collection

Studies were conducted from April to October in 2 con-

secutive years (2014–2015) at Houhatai (42°23.613'N, 116°06.524'E, altitude 1300 m), approximately 25 km north of Shangdu, Zhenglan Qi, Inner Mongolia, China. The habitat of the study site is typical steppe. Our trapping plot was situated on a 2-ha (100 × 200 m) grassland with a mixture of vegetation, such as *Leymus chinensis*, *Artemisia sieversiana*, *Thalictrum petaloideum*, *Stellera chamaejasme*, *Serratula centauroides* and *Heteropappus altaicus*, which provided food or cover for gerbils. No livestock was grazed at the study site during our study.

The mark–recaptures were carried out from 29 April to 24 October 2014 and from 4 May to 19 October 2015, at 2-week intervals. Each trapping session lasted for 3 consecutive days. We trapped Mongolian gerbils using wire-mesh live traps (28 × 13 × 10 cm) and baited with fresh peanuts. We used the concentric circle trapping method for enhancing trappability (Liu *et al.* 2007). Traps were set at 0500–0600 hours from May to August and checked every 1–2 hours until approximately 1100 hours. To avoid trap mortality by heat, we closed traps between 1100 and 1500 hours, resumed at 1600 hours and continued to 1900 hours. Trapping started at approximately 0700 hours and continued to 1730 hours in September and October, and the traps were checked every 1–2 hours. All captured gerbils were toe-clipped at initial capture for permanent identification. Our trapping and handling of Mongolian gerbils was approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, Chinese Academy of Sciences (Ethical Inspection License No:IOZ13047).

We considered gerbils captured in the same burrow system in 2 consecutive trapping sessions to be members of the same social group (Ågren *et al.* 1989a). Hence, we considered that emigration had occurred if a gerbil was not caught at the original burrow system for 2 consecutive trapping sessions or more. Each gerbil was assigned to a social group based on the consecutive trapping data during a specific life-history stage. If a gerbil emigrated from a social group before July, we assigned this gerbil to the latter burrow system during the breeding season. In contrast, if a dispersal occurred in July or August, the gerbil was assigned to the original burrow system during the breeding season. A similar assignment procedure was applied during the food-hoarding season.

Social association matrix

We used the ASNIPE package (Farine & O'Hara 2013) to generate networks based on trapping data and to calculate the simple ratio index (*SRI*) (Ginsberg

& Young 1992) for each pair of individuals during the breeding season and food-hoarding season in both years. The simple ratio index is defined as the number of times that 2 individuals were caught together at the same burrow system at the same recapture incident divided by the total number of times they were caught at the same or different burrows ($SRI = N / (N + N_a + N_b + N_{ab})$); N , times A and B were caught together; N_a , times that only A was caught; N_b , times that only B was caught; N_{ab} , times that A and B were both caught in separate burrow systems). Therefore, the simple ratio index reflects the burrow usage overlap between any 2 individuals (ranging from 0 to 1, where 0 indicates that they never associate and 1 indicates that the dyad was always together) (Wey *et al.* 2013). We constructed an undirected, weighted social network for each season. Thickness of edges in the sociogram corresponded to the simple ratio index value, which reflected the strength of association between any 2 gerbils.

Quantifying social attributes

We calculated assortativity for each season to determine whether associations were stronger within social groups using the ASSORTNET package (Farine 2014).

We also calculated 4 social attributes for each individual in each social network:

1. Social differentiation (the coefficient of variation of association strength, CV): The standard deviation of the mean association strength. Strength was computed as the sum of edge weights (Whitehead 2008). A higher CV value indicates relatively stronger variation in association strength with other individuals.
2. Degree centrality: Based on the number of direct connections an individual has. An individual with a high degree centrality has more influence on those around it (i.e. a more central position).
3. Closeness centrality: The inverse of the shortest path length between the focal individual and every other individual (Freeman 1979). Closeness centrality reflects both direct and indirect connections. An individual with higher closeness has the potential to more quickly spread information or participate in events in the social network.
4. Betweenness centrality: The proportion of shortest path lengths between every pair of other group members on which the focal individual edges (Freeman 1979). Individuals with high betweenness are important for social connections and stability. The removal of high-betweenness individuals will likely fragment or destroy network connectivity (Lusseau & Newman 2004; Wey *et al.* 2008).

Centrality was calculated using the IGRAPH package (Csardi & Nepusz 2006), and these 3 centralities were normalized to facilitate comparisons across networks of different sizes. Social differentiation was calculated using weighted networks, whereas assortativity and degree, closeness and betweenness centrality were calculated using binary networks.

Statistical analysis

We used generalized linear mixed models (GLMMs) to investigate whether social attributes were influenced by sex and season. Each model contained sex, season and their interactions as well as sex and season as fixed effects. Random effects were individual identity and year.

Because social attributes in a network are non-independent (Croft *et al.* 2011), we determined significance in statistical tests (assortativity and GLMMs) by comparing the coefficients of the models (or the test statistic in the case of assortativity) fitted to the observed data with coefficients calculated on 1000 permutations of the network (Farine & Whitehead 2015). Permutations were performed using the ASNIPE package (Farine & O'Hara 2013) following the algorithm originally described by Bejder *et al.* (1998). This method enabled us to restrict the random swaps in the data stream so that swaps between pairs that were captured on the same trapping day were limited. We performed 1000 iterations of randomizations and then calculated the same social attributes

and conducted the same analysis for each permuted network that we did for the observed data. *P*-values were calculated by comparing the coefficient from the model based on the observed data with the coefficients from the same model based on the randomized data (herein P_{rand}) (Farine & Whitehead 2015). A result was considered significant if the observed coefficient fell outside the 95% range of the random coefficient distribution (Leu *et al.* 2016).

Generalized linear mixed models were analyzed using the LME4 package (Bates *et al.* 2013). All statistical analyses were performed using R software (R Core Team 2015).

RESULTS

There were 48 total trapping days (33 days during the breeding season and 15 days during the food-hoarding season) in 2014 and 42 trapping days (28 days during the breeding season, 14 days during the food-hoarding season) in 2015. The average number of catches per gerbil was 6 during the breeding season and 8 during the food-hoarding season in 2014 and 4 during the breeding season and 3 during the food-hoarding season in 2015. Only individuals trapped at least 3 times during each season were included in network and subsequent analyses to exclude wanderers and those sampled by chance; this procedure resulted in 137 females and 116 males in 2014 and 26 females and 27 males in 2015 for analysis.

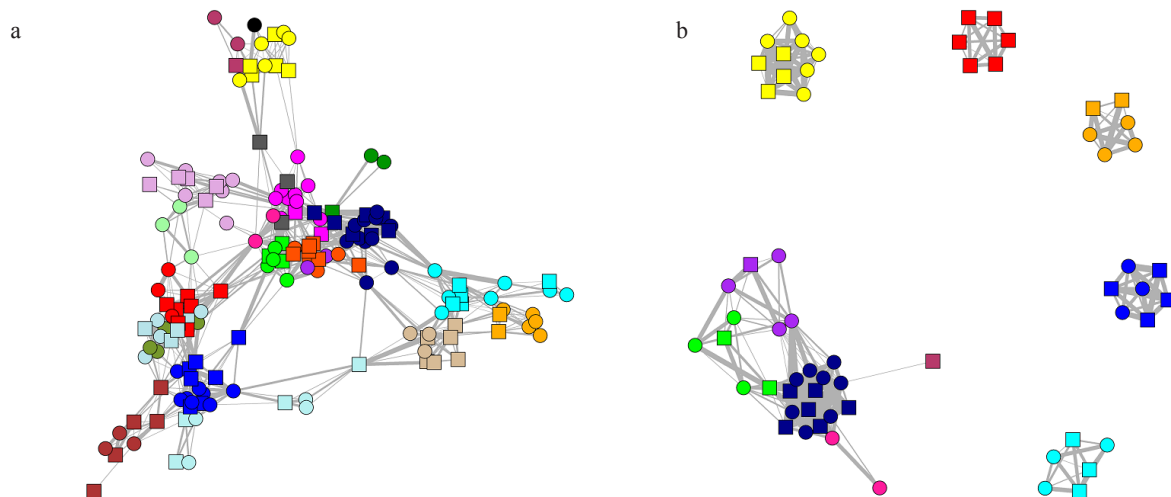


Figure 1 Association networks of Mongolian gerbils during: (a) breeding and (b) food-hoarding season in 2014. Females are represented as circles and males as squares. Colors represent borrow systems. Thickness of edges corresponds to the *SRI* value, which reflects the strength of association.

Social association at the network level

As expected, inter-group social associations were more frequent during the breeding season than during the food-hoarding season (Fig. 1). Accordingly, the assortment coefficients for social groups during the breeding season were 0.774 and 0.663, while they were 0.801 and 1 during the food-hoarding season. Thus, the so-

cial group assortativity during the food-hoarding season was higher than that during the breeding season in both years, and the permutations showed that the observed assortment coefficient was significantly higher than expected by chance during all periods ($P_{\text{rand}} = 0.001$, $P_{\text{rand}} < 0.001$ for breeding season and $P_{\text{rand}} < 0.001$, $P_{\text{rand}} < 0.001$ for food-hoarding season, Fig. 2).

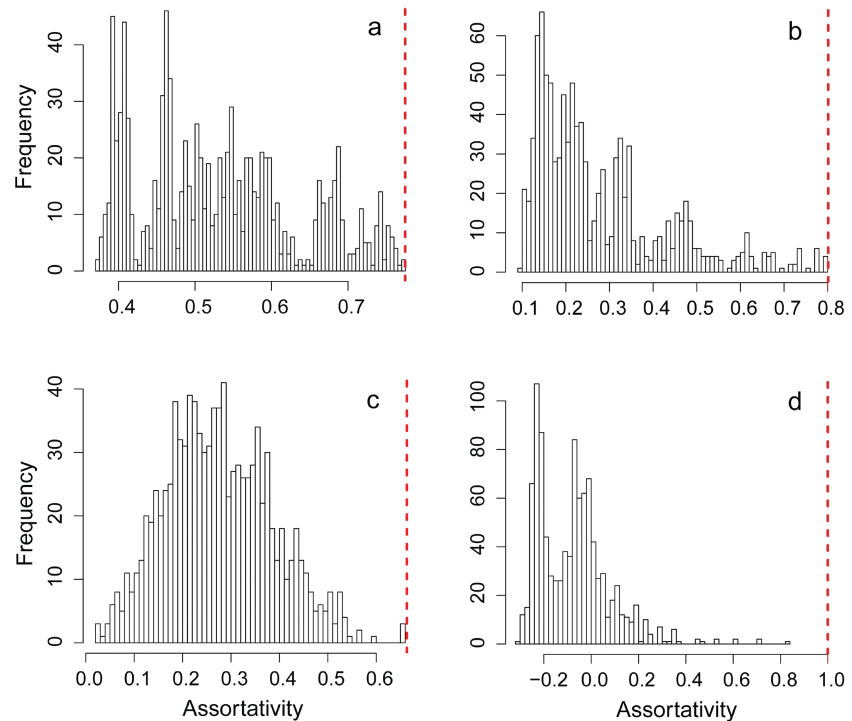


Figure 2 Assortment coefficient differed from those expected by chance: comparison of the assortment coefficient based on the observed data (dashed vertical line) and the frequency distribution of assortment coefficient based on the randomized data: (a) breeding season in 2014, (b) food-hoarding season in 2014, (c) breeding season in 2015 and (d) food-hoarding season in 2015.

Table 1 Generalized linear mixed models testing the effects of sex, season and their interaction on 4 social attributes

Social attribute	Factor	Coefficient	SE	<i>t</i>	P_{rand}
Social differentiation	Sex	-0.007	0.004	-1.675	0.051
	Season	0.006	0.005	1.031	0.015**
	Sex × Season	0.007	0.008	0.908	0.391
Degree	Sex	0.007	0.010	0.667	0.381
	Season	0.126	0.014	9.026	<0.0001**
	Sex × Season	-0.051	0.020	-2.485	0.035**
Closeness	Sex	0.002	0.010	0.252	0.145
	Season	-0.209	0.013	-15.360	0.001**
	Sex × Season	-0.0006	0.019	-0.034	0.025**
Betweenness	Sex	0.007	0.005	1.451	0.100
	Season	-0.001	0.007	-0.220	0.001**
	Sex × Season	-0.018	0.010	-1.766	0.023**

†The GLMM formula in R was `lmer(social differentiation~sex × season + (1|year) + (1|ID))`, and respectively for other dependent variables. **These factors were significant at the 0.05 level.

Effects of sex and season on social attributes

The GLMMs revealed that there was no significant difference in social differentiation or degree, closeness or betweenness centrality between male and female ger-

bils (Table 1, Fig. 3). In contrast, there was a significant difference in these 4 social attributes between breeding and food-hoarding season (Table 1, Fig. 3).

Gerbils had significantly higher social differentiation

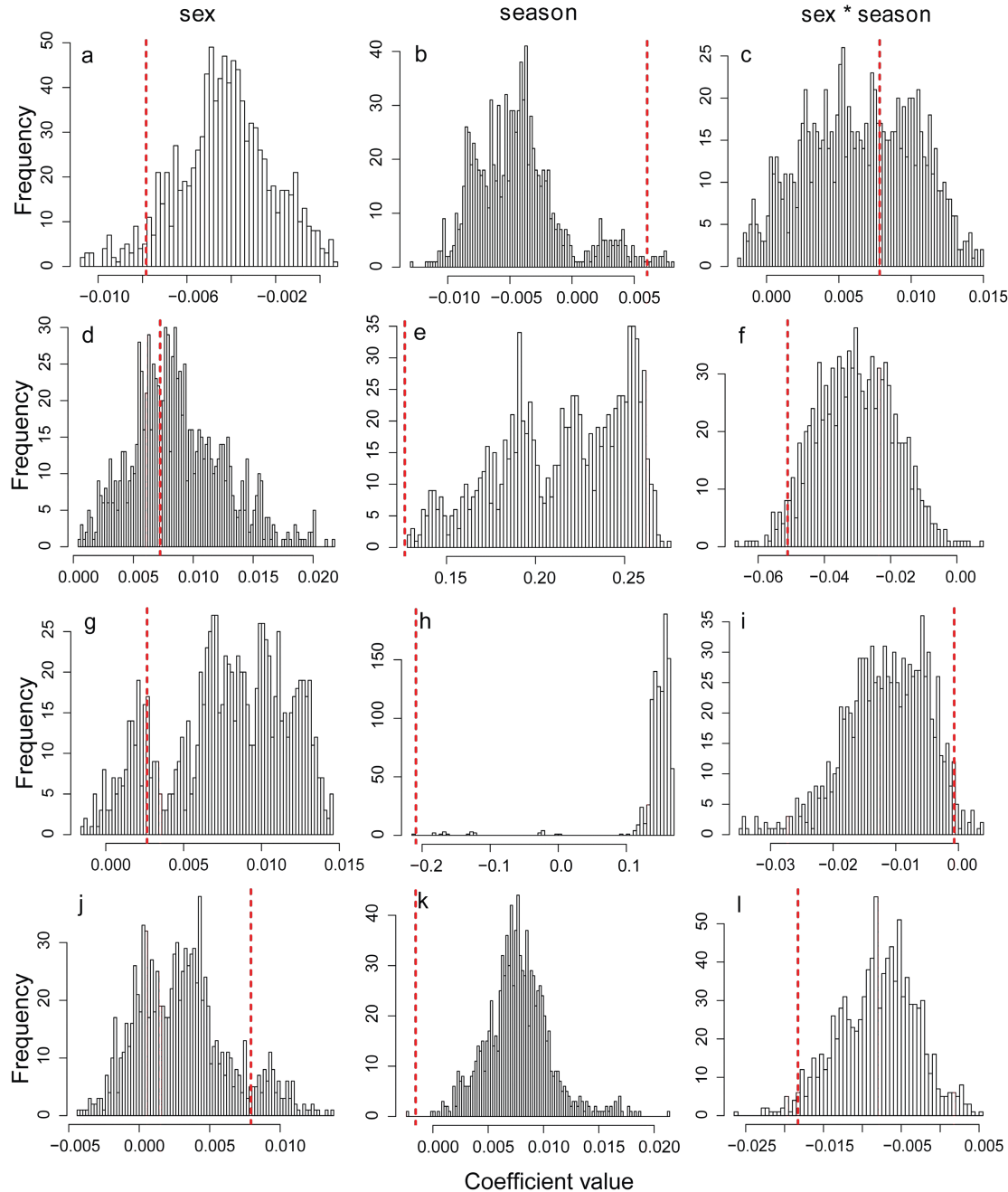


Figure 3 Comparison of the coefficient from the generalized linear mixed models based on the observed data (dashed vertical line) and the frequency distribution of coefficients from the same model based on the randomized data: (a–c) social differentiation, (d–f) degree, (g–i) closeness and (j–l) betweenness.

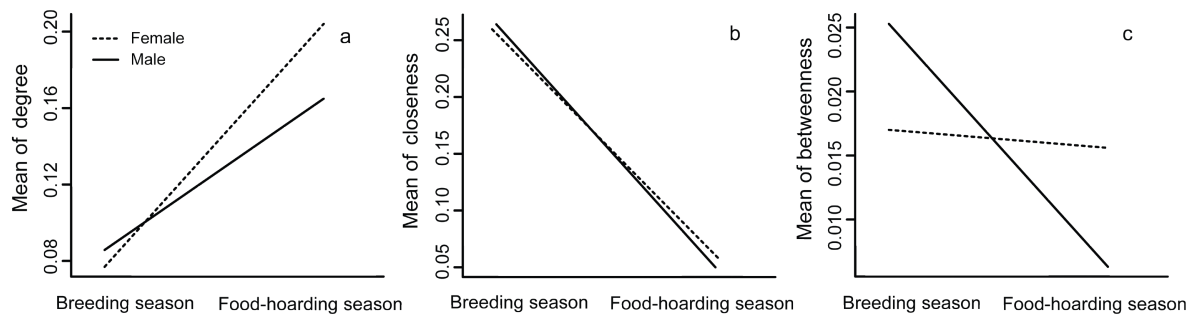


Figure 4 The interaction effects between sex and season for: (a) degree, (b) closeness and (c) betweenness.

($t = 1.031$, $P_{\text{rand}} = 0.015$) and degree centrality ($t = 9.026$, $P_{\text{rand}} < 0.0001$) during the food-hoarding season than during the breeding season (Table 1, Fig. 3). Moreover, there was a significant interaction between sex and season for degree centrality ($P_{\text{rand}} = 0.035$), suggesting that the increase in direct social partners was greater for females compared to males (Table 1, Fig. 4a). In addition, gerbils had significantly lower closeness ($t = -15.360$, $P_{\text{rand}} = 0.001$) and betweenness ($t = -0.220$, $P_{\text{rand}} = 0.001$) centrality during the food-hoarding season than during the breeding season (Table 1, Fig. 3). The significant interaction effects of sex and season on closeness ($P_{\text{rand}} = 0.025$) and betweenness ($P_{\text{rand}} = 0.023$) indicated that the decrease in these 2 centralities was larger for males compared to females (Table 1, Fig. 4b,c).

DISCUSSION

As we expected, the inter-group associations of Mongolian gerbils decreased significantly during the food-hoarding season. This finding supports the hypothesis that overlapped home ranges may facilitate reproductive associations between inter-group individuals during the breeding season (Wang *et al.* 2011), and the enhanced within-group associations during the food-hoarding season may be related to cooperative hoarding.

The food-hoarding period is considered a crucial life-history stage for non-hibernating small rodents in temperate areas, as sufficient food reserves can improve an individual's overwinter survival (Kuhn & Vander Wall 2008; Morrison *et al.* 2009) and recruitments in early spring (Vessey & Vessey 2007). Consequently, individuals commonly enhance their territoriality to defend food in that situation (Wolff 2007). Because home-range size is positively related to social size in Mongolian gerbils (Ågren *et al.* 1989a; Wang *et al.*

2011), and experimental study has demonstrated that winter food availability limits gerbils' winter survival (Liu *et al.* 2011), we believe that enhanced associations within groups during the food-hoarding season contributes to winter survival of entire family groups. Moreover, the assortment coefficients differed from those expected by chance, suggesting that Mongolian gerbils adjust their association strategies to adapt to various requirements at different life-history stages.

At the individual level, the enhanced degree centrality and social differentiation suggest that gerbils have more partners and stronger differentiation of the strength of associations during the non-breeding season than during the breeding season. Generally, animals benefit from preferred associations. For instance, kin-biased associations enhance the insect capture rate in squirrel monkeys (*Saimiri sciureus macrodon* Linnaeus, 1758) (Montague *et al.* 2014). Alternatively, a study of house mice (*Mus domesticus* Linnaeus, 1758) indicate that individuals that mate with preferred partners have higher productive success than those that mate with non-preferred partners (Drickamer *et al.* 2003). Interestingly, the social differentiation during the breeding season was significantly lower than that during the food-hoarding season in Mongolian gerbils; this observation may be consistent with their life-history traits. Larger gerbils dominate smaller ones (Ågren *et al.* 1989a), and females inhibit one another's reproductive development (Clark & Galef 2001). Therefore, gerbils that have no reproductive opportunities may enter neighboring territories and solicit copulations from the resident male, leading to a relatively homogeneous strength of associations. In contrast, social associations are mostly restricted to intra-group associations during active collection and food hoarding.

In addition, we found that closeness and betweenness centrality decreased significantly during the food-hoard-

ing season. This result not only indicates that there may be an inevitable loss of control over other individuals in the network but also reflects a decrease in the connectivity of social networks. In general, frequent association with individuals in other social groups provides opportunities for extra mating (Nichols *et al.* 2015), consistent with the results for Mongolian gerbils in the present study. In some cases, however, animals seem to avoid participating in more social associations to avoid the costs of increased sociality (e.g. yellow-bellied marmots *Marmota flaviventris*: Maldonado-Chaparro *et al.* 2015). Li and Wang (2005) report that in Mongolian gerbils, thermogenic capacity and maintenance costs increased during cold acclimation. Consequently, decreased inter-group associations during the food-hoarding season may be beneficial to reduce gerbils' energy expenditure. Individuals with high closeness or betweenness centrality (i.e. central individuals in the network) usually have high social status (e.g. chimpanzee *Pan troglodytes* versus Blumenbach, 1775: Kanngiesser *et al.* 2011) and higher fitness than others, such as enhanced longevity (Silk *et al.* 2010) or higher reproductive success (Cameron *et al.* 2009; Bar Ziv *et al.* 2016). Thus, further studies should focus on how gerbils benefit from seasonal variation in centrality with respect to increasing survival and reproduction and reducing energy expenditure.

Sex differences in patterns of social association are common (Ruckstuhl 2007; Holekamp *et al.* 2012; Ma *et al.* 2014). Unexpectedly, we found no significant sex differences in social differentiation or degree, closeness and betweenness centrality. This result supports the hypothesis that sex may not play any role in determining social networks (Wey & Blumstein 2010). One possible reason is that although male gerbils usually dominate female gerbils (Ågren *et al.* 1989a), they cannot prevent partner females from leaving their territories to copulate with the neighboring males during the breeding season (Ågren *et al.* 1989a). In contrast, during the food-hoarding season, most group members take part in storing food (Ågren *et al.* 1989b), and both males and females show high aggression against out-group members during this period (Deng *et al.*, unpublished data). Furthermore, because our investigation was based on mark-recapture data, it is possible that the results of this study provide limited insight into the lack of sex difference.

Nevertheless, we found significant interaction effects of sex and season on degree, closeness and betweenness centrality. This finding indicates that although individuals have similar responses to seasonal changes in so-

cial influence, the intensity of the changes differs significantly according to sex. Specifically, the increase in the number of direct social partners was higher and the decrease in influence over other individuals was smaller for females than that for males during the food-hoarding season, suggesting that compared to males, female gerbils have a relatively higher influence over other individuals during the food-hoarding period.

In summary, our results suggest that Mongolian gerbils reduce their inter-group associations and social influence over others during the food-hoarding season and that female gerbils are relatively more important than male gerbils for maintaining social cohesion during the food-hoarding season. Social network position or social network structure has fitness consequences, including effects on survival (Silk *et al.* 2009, 2010), reproductive success (Cameron *et al.* 2009; Wey & Blumstein 2012) and family fitness (Royle *et al.* 2012). However, it remains unclear how gerbils benefit from seasonal social associations. Consequently, future studies will have to address these questions, which require long-term demographic investigation.

ACKNOWLEDGMENTS

We are grateful to all the members of the Animal Physiological Ecology Group for helpful discussions. We would like to thank Mr Bin Wu and colleagues from the Plant Protection Station of Taipusiqi for help with fieldwork. Special thanks to Demien R. Farine for providing invaluable help in the social network analysis. The present study was financially supported by the National Natural Science Foundation of China (No. 31372211) to WL and the Chinese Academy of Sciences (KSCX2-EW-N-005) to DHW.

REFERENCES

- Ågren G, Zhou Q, Zhong W (1989a). Ecology and social-behavior of Mongolian gerbils, *Meriones-unguiculatus*, at Xilinhot, Inner-Mongolia, China. *Animal Behaviour* **37**, 11–27.
- Ågren G, Zhou Q, Zhong W (1989b). Territoriality, cooperation and resource priority – Hoarding in the Mongolian gerbil, *Meriones-unguiculatus*. *Animal Behaviour* **37**, 28–32.
- Arseneau-Robar TJM, Taucher AL, Schnider AB, van Schaik CP, Willems EP (2017). Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. *Animal Behaviour* **123**, 129–37.

- Bar Ziv E, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L (2016). Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. *Behavioral Ecology and Sociobiology* **70**, 901–12.
- Bates D, Maechler M, Bolker B (2013). Linear mixed-effect models using S4 classes. R package. Available from URL: <http://CRAN.R-project.org/package=lme4>.
- Bejder L, Fletcher D, Brager S (1998). A method for testing association patterns of social animals. *Animal Behaviour* **56**, 719–25.
- Bulter RG (1980). Population size, social behaviour, and dispersal in house mice: A quantitative investigation. *Animal Behaviour* **28**, 78–85.
- Cameron EZ, Setsaas TH, Linklater WL (2009). Social bonds between unrelated females increase reproductive success in feral horses. *PNAS* **106**, 13850–53.
- Clark MM, Galef BG (2001). Socially induced infertility: familial effects on reproductive development of female Mongolian gerbils. *Animal Behaviour* **62**, 897–903.
- Crockett CM, Eisenberg JF (1987). Howlers: variation in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RR, Struhsker TT, eds. *Primate Societies*. The University of Chicago Press, Chicago, IL.
- Croft DP, James R, Ward AJW, Botham MS, Mawdsley D, Krause J (2005). Assortative interactions and social networks in fish. *Oecologia* **143**, 211–9.
- Croft DP, Madden JR, Franks DW, James R (2011). Hypothesis testing in animal social networks. *Trends in Ecology & Evolution* **26**, 502–7.
- Csardi G, Nepusz T (2006). The IGRAPH software package for complex network research. *International Journal of Complex Systems*.
- Drickamer LC, Gowaty PA, Wagner DM (2003). Free mutual mate preferences in house mice affect reproductive success and offspring performance. *Animal Behaviour* **65**, 105–14.
- Farine DR (2014). Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Animal Behaviour* **89**, 141–53.
- Farine DR, O'Hara RB (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution* **4**, 1187–94.
- Farine DR, Whitehead H (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology* **84**, 1144–63.
- Freeman LC (1979). Centrality in social networks conceptual clarification. *Social Networks* **1**, 215–39.
- Ginsberg JR, Young TP (1992). Measuring association between individuals or groups in behavioral studies. *Animal Behaviour* **44**, 377–9.
- Hirsch BT (2011). Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition. *Behavioral Ecology and Sociobiology* **65**, 391–9.
- Holekamp KE, Smith JE, Strelhoff CC, Van Horn RC, Watts HE (2012). Society, demography and genetic structure in the spotted hyena. *Molecular Ecology* **21**, 613–32.
- Kanngiesser P, Sueur C, Riedl K, Grossmann J, Call J (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology* **73**, 758–67.
- Krause J, Lusseau D, James R (2009). Animal social networks: an introduction. *Behavioral Ecology and Sociobiology* **63**, 967–73.
- Krause J, Ruxton GD (2002). *Living in Groups*. Oxford University Press, New York.
- Krebs CJ (2015). One hundred years of population ecology: Successes, failures and the road ahead. *Integrative Zoology* **10**, 233–40.
- Kuhn KM, Vander Wall SB (2008). Linking summer foraging to winter survival in yellow pine chipmunks (*Tamias amoenus*). *Oecologia* **157**, 349–60.
- Kurvers RHJM, Adamczyk VMAP, Kraus RHS *et al.* (2013). Contrasting context dependence of familiarity and kinship in animal social networks. *Animal Behaviour* **86**, 993–1001.
- Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M (2014). The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends in Ecology & Evolution* **29**, 326–35.
- Leu ST, Farine DR, Wey TW, Sih A, Bull CM (2016). Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards. *Animal Behaviour* **111**, 23–31.
- Li GL, Hou XL, Wan XR, Zhang ZB (2016). Sheep grazing causes shift in sex ratio and cohort structure of Brandt's vole: Implication of their adaptation to food shortage. *Integrative Zoology* **11**, 76–84.

- Li XS, Wang DH (2005). Seasonal adjustments in body mass and thermogenesis in Mongolian gerbils (*Meriones unguiculatus*): The roles of short photoperiod and cold. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* **175**, 593–600.
- Liu W, Wan X, Zhong W (2007). Population dynamics of the Mongolian gerbils: seasonal patterns and interactions among density, reproduction and climate. *Journal of Arid Environments* **68**, 383–97.
- Liu W, Wang GM, Wang YN, Zhong WQ, Wan XR (2009). Population ecology of wild Mongolian gerbils *Meriones unguiculatus*. *Journal of Mammalogy* **90**, 832–40.
- Liu W, Wang GM, Wan XR, Zhong WQ (2011). Winter food availability limits winter survival of Mongolian gerbils (*Meriones unguiculatus*). *Acta Theriologica* **56**, 219–27.
- Lusseau D, Newman MEJ (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B-Biological Sciences* **271**, S477–81.
- Ma ST, Resendez SL, Aragona BJ (2014). Sex differences in the influence of social context, salient social stimulation and amphetamine on ultrasonic vocalizations in prairie voles. *Integrative Zoology* **9**, 280–93.
- Makagon MM, McCowan B, Mench JA (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science* **138**, 152–61.
- Maldonado-Chaparro AA, Hubbard L, Blumstein DT (2015). Group size affects social relationships in yellow-bellied marmots (*Marmota flaviventris*). *Behavioral Ecology* **26**, 909–15.
- Mitani JC, Watts DP, Amsler SJ (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology* **20**, R507–8.
- Montague MJ, Disotell TR, Di Fiore A (2014). Population genetics, dispersal, and kinship among wild squirrel monkeys (*Saimiri sciureus macrodon*): Preferential association between closely related females and its implications for insect prey capture success. *International Journal of Primatology* **35**, 169–87.
- Morrison SF, Pelchat G, Donahue A, Hik DS (2009). Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia* **159**, 107–16.
- Nichols HJ, Cant MA, Sanderson JL (2015). Adjustment of costly extra-group paternity according to inbreeding risk in a cooperative mammal. *Behavioral Ecology* **26**, 1486–94.
- Owen MA, Swaisgood RR, Blumstein DT (2017). Contextual influences on animal decision-making: Significance for behavior-based wildlife conservation and management. *Integrative Zoology* **12**, 32–48.
- Pinter-Wollman N, Hobson EA, Smith JE *et al.* (2014). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology* **25**, 242–55.
- R Core Team (2015). R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: <http://www.R-project.org>.
- Royle NJ, Pike TW, Heeb P, Richner H, Kolliker M (2012). Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society B-Biological Sciences* **279**, 4914–22.
- Ruckstuhl KE (2007). Sexual segregation in vertebrates: Proximate and ultimate causes. *Integrative and Comparative Biology* **47**, 245–57.
- Silk JB, Beehner JC, Bergman TJ *et al.* (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B-Biological Sciences* **276**, 3099–104.
- Silk JB, Beehner JC, Bergman TJ *et al.* (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology* **20**, 1359–61.
- Smith JE, Van Horn RC, Powning KS *et al.* (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology* **21**, 284–303.
- Vessey SH, Vessey KB (2007). Linking behavior, life history and food supply with the population dynamics of white-footed mice (*Peromyscus leucopus*). *Integrative Zoology* **2**, 123–30.
- Walker FM, Taylor AC, Sunnucks P (2008). Female dispersal and male kinship-based association in southern hairy-nosed wombats (*Lasiorninus latifrons*). *Molecular Ecology* **17**, 1361–74.
- Wang Y, Liu W, Wang G, Wan X, Zhong W (2011). Home-range sizes of social groups of Mongolian gerbils *Meriones unguiculatus*. *Journal of Arid Environments* **75**, 132–7.

- Wey T, Blumstein DT, Shen W, Jordán F (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* **75**, 333–44.
- Wey TW, Blumstein DT (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour* **79**, 1343–52.
- Wey TW, Blumstein DT (2012). Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology* **66**, 1075–85.
- Wey TW, Burger JR, Ebensperger LA, Hayes LD (2013). Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour* **85**, 1407–14.
- Whitehead H (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago: University of Chicago Press.
- Wolff JO (2007). Social biology of rodents. *Integrative Zoology* **2**, 193–204.

Cite this article as:

Deng K, Liu W, Wang D (2017). Inter-group associations in Mongolian gerbils: Quantitative evidence from social network analysis. *Integrative Zoology* **12**, 446–56.