Original Article

Dyadic associations and individual sociality in bighorn ewes

Eric Vander Wal,[a,b] Audrey Gagné-Delorme,[a] Marco Festa-Bianchet,[a] and Fanie Pelletier[a]

[a]Département de biologie, Université de Sherbrooke, 2500 boul. de l'Université, Sherbrooke, Québec J1K 2R1, Canada and [b]Department of Biology, Memorial University of Newfoundland, 232 Elizabeth Avenue, St. John's, Newfoundland A1B 3X9, Canada

Sociality presumably evolved because it leads to fitness benefits; yet we know little about what drives individual variability in sociality, particularly with respect to hierarchical levels of social organization. Social network architecture is based upon dyadic interactions, but the factors affecting pairwise relationships are not necessarily those affecting higher-level network-derived measures of social behavior. We examined the influence of relatedness, age, dominance, and reproductive status on proximal associations and social network centrality of individuals in the fission–fusion society of bighorn ewes (*Ovis canadensis*) at Ram Mountain, Canada. From 2011 to 2013, 63–81% of adult ewes were equipped with proximity loggers, recording when they were within 1.5 m of one another. Ewe social structure was not random and individuals exhibited a tendency to have proximal associations that were consistent across years. Age and reproductive status appeared to have a weak effect on network centrality, but this effect was largely absent for frequency of proximal association. Furthermore, we found no effect of dominance rank on either proximal associations or network centrality. We speculate that interannual variation in these relationships may be indicative of predation affecting social dynamics. The disconnect between determinants that affect the costs and benefits of dyadic associations and those that emerge from network-derived behaviors highlights the importance of testing effects at multiple levels of social organization in animal societies.

Key words: **bighorn sheep, dominance rank, fission–fusion, kinship, social network.**

INTRODUCTION

Group living can affect individual fitness (Silk 2007; Ebensperger et al. 2012). One benefit of group living is increased collective vigilance and predator dilution (Rieucau and Martin 2007). Group living thus necessitates some form of dyadic associations, and variation in sociality among individuals should affect fitness. In some instances, it has been shown to do just that: social bonds improved reproductive success of feral mares (Cameron et al. 2009) and access to social partners increased foal survival in another study of feral horses (Nunez et al. 2015). Social associations lead to complex networks of direct and indirect pairwise relationships (Brent 2015). The architecture of social connectivity networks that results from associations affects survival in manakins (*Chiroxiphia linearis* [McDonald 2007] and dolphins [*Tursiops* spp.—Stanton and Mann 2012]). In bighorn sheep (*Ovis canadensis*), sociality in adult females is correlated with survival and reproductive success (Vander Wal et al. 2015). Although we are learning more about the fitness consequences of social connectivity, we know comparatively little about what factors determine patterns of dyadic associations and the resulting pattern of network connectivity—particularly in fission–fusion societies. Indeed, recent reviews highlighted the importance of understanding variation in behavior of individuals within networks (Pinter-Wollman et al. 2014) and the importance of network structure on social evolution (Kurvers et al. 2014). However, we do not know whether the factors, or putative selective pressures, that determine patterns at one level of social organization differ from those that affect other levels in the network hierarchy, for example, dyad versus network.

Many social structures have been quantified using social networks built from dyadic associations. The factors affecting these associations, however, may differ from those affecting network-derived measures of sociality (Sih et al. 2009). For example, if individuals preferred to associate with relatives, analyses of dyadic associations may reveal an effect of relatedness. If gregariousness was important for survival and many individuals had few or no relatives in the population, however, network-level analyses may not suggest any effect of kinship. Few studies have examined what ecological factors shape dyadic relationships (Archie et al. 2008), whose strength

Address correspondence to M. Festa-Bianchet. E-mail: m.festa@usher-brooke.ca.

can vary substantially within a population (Wey et al. 2008). The causes of this variation have rarely been explored through social network analysis (Lusseau and Newman 2004). Here, we apply social network analyses to exceptionally detailed dyadic association data from a population of bighorn sheep where a majority of adult ewes were monitored with proximity collars for 3 years to explore what ecological and social variables affect associations. We also tested whether network-derived, individual-based behaviors and dyadic associations were affected by the same factors.

Kin selection is often invoked as an evolutionary explanation of cooperation (Grafen 1984), because cooperation among kin leads to direct benefits for the receiver and indirect benefits for the provider. Although kin selection appears to affect the behavior of many primates (Silk 2002), eusocial insects (Hughes et al. 2008), and birds (Krakauer 2005), in many social systems cooperation cannot be explained solely through kin selection (Clutton-Brock 2002). Little is known about the role of kinship in the social behavior of female large herbivores. In some species, social groups are often composed of relatives; for example, in red deer (*Cervus elaphus*) (Albon et al. 1992) and wild boars (*Sus scrofa*) (Podgórski et al. 2014). However, in many other species, group composition appears independent of kin relationships, for example, bighorn sheep (Festa-Bianchet 1991); elk, *Cervus canadensis* (Vander Wal et al. 2012); and feral horses (Cameron et al. 2009). For instance, the benefits of detecting and diluting predation risk may require a larger group than can be achieved by related individuals alone. Therefore, a choice of preferred associates can also be beneficial without kinship or cooperation. Furthermore, by associating with familiar individuals, animals may decrease the time allocated to social vigilance (Griffiths et al. 2004) or reduce competition (Clutton-Brock and Huchard 2013). Similarly, avoidance of aggressive individuals can decrease the risk of injuries and the cost of agonistic interactions (Ehardt and Bernstein 1987).

We sought to first determine the genetic, age, dominance, and reproductive factors affecting variation in sociality in bighorn ewes and then test whether these differ for fine-scale dyadic associations or individual-level network metrics of centrality. Specifically, we tested a series of predictions derived from 4 hypotheses.

P$_1$: The relatedness hypothesis derived from kin selection theory predicts that related ewes will be more likely to form close associations than unrelated ewes.

P$_2$: The demography hypothesis predicts that similarity in age would increase the frequency of association. Individuals of similar age might be more familiar with each other because they interacted since early development (Sih et al. 2009). For example, age is a determinant of social structure in elephants (*Loxodonta africana*, Wittemyer et al. 2005).

P$_3$: We predicted stronger associations among individuals of similar rank for 2 reasons. First, aggressive interactions between a high- and a low-ranked individual may involve a risk of injury for the subordinate. Therefore, low-ranked ewes may avoid risk by associating with other subordinates. Second, animals of similar ranks may seek opportunities to interact with each other to increase in rank or to maintain their status (Archie et al. 2006; Smith et al. 2007).

P$_4$: Reproductive status may affect dyadic associations, because lambs face greater predation pressure than adults, and lactating ewes trade-off vigilance and food acquisition (Rieucau and Martin 2007). Lactating ewes may benefit from forming groups to share vigilance and increase the dilution effect among lambs in case of a predator attack. Hence, we predict that similarity in reproductive status will increase the frequency of association (Vander Wal et al. 2015).

METHODS

Bighorn sheep at Ram Mountain have been monitored since 1971 (Jorgenson et al. 1997). Each year, from late May to late September, sheep are captured in a corral trap baited with salt. All individuals considered in this study were first captured as lambs, individually marked and accounted for annually. Therefore, their age was known. A tissue sample is collected at first capture. All animals are genotype at 32 microsatellites markers and paternity is assessed using CERVUS (see Coltman et al. 2005; Poissant et al. 2008 for more information on the molecular analyses). We matched mother–offspring pairs by observation of nursing behavior and confirmed these pairs by comparison of molecular data. Here, we use data collected from 2011 to 2013 on adult ewes. Based on the pedigree, we calculated the pairwise coefficient of relatedness with the R package *nadiv* (Wolak 2012). This coefficient ranged between 0 and 0.62. Although mother–daughter pairs should have a relatedness of 0.5, inbreeding meant that 8/411 pairs had kinship values >0.5 (Rioux-Paquette et al. 2010). We knew both parents for all ewes except 3 that were introduced from elsewhere and therefore were unrelated to the residents and not in the pedigree. These ewes were assigned a relatedness value of 0. Ewes were captured on average 4 times each year. Female reproductive status was also evaluated by examining the teats, to identify ewes that gave birth (presence of milk) but lost their lamb soon afterwards.

We established the dominance hierarchy among ewes by direct observation of agonistic interactions (Favre et al. 2008). We used the procedure described in De Vries (1998) implemented in *MatMan 1.1* (De Vries et al. 1993) to minimize the number and strength of inconsistencies. We then constructed a matrix of relative rank differences for each dyad (Table 1). We standardized dominance rank as $1 - (\text{rank}/Nx)$, were Nx is the number of ewes in year x, so that relative rank was not affected by yearly sample size (Pelletier and Festa-Bianchet 2006). The linearity index h' (De Vries et al. 1993) varies between 0 and 1, 1 being perfectly linear. A randomization procedure (10 000 randomizations) suggested that the h' index was significantly linear in 2 of the 3 years, confirming previous findings of a linear dominance hierarchy in this species (Favre et al. 2008). The directional consistency index (DCI) estimates the predictability in the outcome of interactions within each dyad. It ranges from 0 to 1, with 0 meaning that the outcome of interactions is unpredictable based on earlier encounters and 1 implying perfect consistency in outcome. For bighorn ewes in this study, the DCI was very strong (Table 1).

We fitted adult females with proximity logger collars (Sirtrack Tracking Solutions, Havelock North, New Zealand). Although we

Table 1

Linearity and consistency of the dominance hierarchy of bighorn ewes at Ram Mountain, 2011–2013

| Year	Females (N)	Interactions observed	% dyads observed	h'[a]	P[b]	DCI
2011	18	83	12.41	0.10	0.330	0.96
2012	25	163	25.38	0.17	0.030	0.98
2013	18	318	53.66	0.32	<0.001	0.97

[a]Linearity index.
[b]P value for linearity.

aimed to have all adult ewes collared, some collars ceased to function. Most ewes aged 2 years and older had a functioning proximity collar (2011: 15/23; 2012: 17/27; 2013: 17/21). Collars recorded proximity events at a distance of 1.5 m or less or approximately one sheep body length. At this distance, social interactions involving contact are possible. Proximity collars registered the identity of the encountered animal and the date, time, and duration (seconds) of each event. As suggested by Prange et al. (2006), we excluded events lasting only 1 s. We also excluded events recorded when sheep were near or in the trap. Proximity collars do not all perfectly record events at the set distance: some register contacts only when individuals are slightly closer, and others have a wider range. Therefore, we corrected for collar bias as proposed by Boyland et al. (2013). To measure strength of association among dyads, we used the number of proximity events between 21 June and 22 August, when all loggers were functioning in all 3 years.

To test the effects of variables of interest on the number of proximity events, we used multiple regressions with matrices (MRM) implemented in the *R* (R Development Core Team 2011) package *ecodist* (Goslee and Urban 2007). The MRM tests the significance of explanatory variables by permutation and allows for more than one explanatory distance matrix (Lichstein 2007). For this study, the matrix of associations is the response variable, while explanatory variables are represented as distant matrices measuring the extent of similarity between dyads (Lichstein 2007). We included a relatedness matrix and coded other variables of interest into dissimilarity matrices. For age or dominance, we calculated the difference in age or rank for each dyad. We tested the effect of similarity of age and dominance rank separately because they are highly correlated (Favre et al. 2008). We used the pairwise coefficient of relatedness based on the pedigree to test the effect of kinship calculated with R package *nadiv* (Wolak 2012). We coded similarity of reproductive status as 1 and dissimilarity as 0. We considered ewes to be nursing a lamb during a summer if they were lactating for at least 2 weeks. For 45 lactating ewe-years in 2011–2013, 84% (*n* = 38) of lambs survived at least 3 months. All *P* values for MRM analyses were calculated based on 10 000 permutations.

To test if matrices representing the social networks were correlated across years (2011–2013), we also used Mantel tests implemented in *ecodist* (Goslee and Urban 2007) for dyads wearing proximity loggers for pairs of consecutive years (90 dyads monitored in 2011 and 2012; 132 monitored in 2012 and 2013). We used Mantel test for 36 dyads that were present for the 3 years. The *P* values for the Mantel test were obtained based on 10 000 permutations.

The social network framework represents social structure graphically and is used to analyze sociality at the individual, dyadic, and network scale (Wey et al. 2008; Croft et al. 2011). We focused on individual metrics of sociality and constructed yearly social networks using package *igraph* (Csardi and Nepusz 2006). Networks were undirected and edges were weighted using the frequency of proximity events standardized by their maximum to represent the strength of relationships within dyads (Figure 1). Standardizing edge weights within year was necessary because the number of proximity events varied across years (Figure 2). From these weighted networks, we calculated the eigenvector centrality and graph strength of all ewes in the network for each year, which represents their individual level of sociality. The eigenvector centrality as a proxy of individual sociality also presents several advantages: it is standardized between 0 and 1, includes both direct and indirect social bonds (Brent 2015), and is less affected by sampling bias (Costenbader and Valente 2003). We repeated network analyses using graph strength, a measure of centrality that does not account
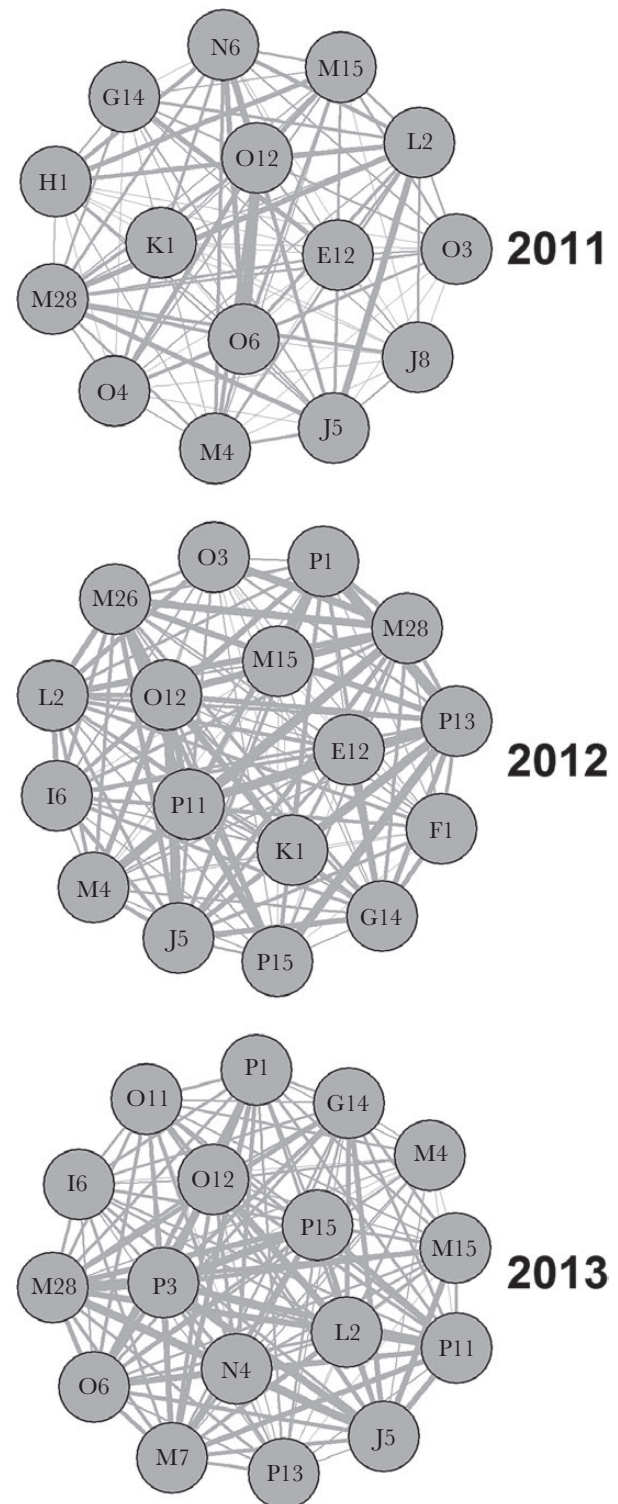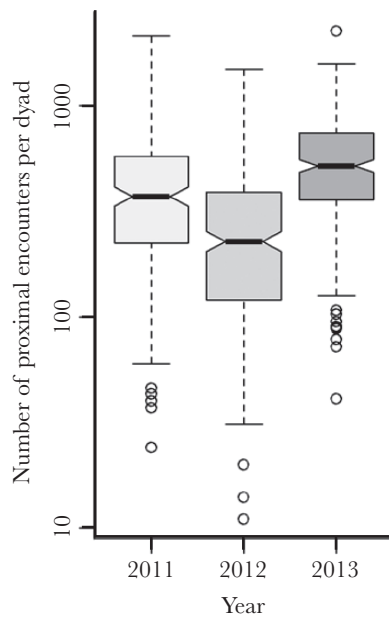

Figure 1
Social networks of bighorn ewes at Ram Mountain, Alberta, 2011–2013. Nodes represent ewe identity and line thickness is proportional to association strength.

for indirect associations and is the summed weights of an individual's edges (Supplementary Tables 1 and 2). In this population, eigenvector centrality and graph strength calculated using long-term data on group membership are correlated with other network measures and with fitness (Vander Wal et al. 2015).

Random associations among individuals may appear nonrandom (Krause et al. 2011). We used 2 approaches to avoid this possibility. Sheep are captured in a trap (see figure 1 in Poissant et al. 2013), and multiple groups can be captured at a given time. Sheep are then weighed, measured, and released individually. Trapping disrupts social groups requiring that individuals then actively re-associate with other sheep. As a result, repeated measures of association in groups or of proximal events are unlikely to occur by chance. To confirm this, we tested whether observed networks differed from those formed if animals associated at random, we created random social networks (Lusseau 2003) from 10 000 permutations of networks' edges (Croft et al. 2011) using package *vegan* (Oksanen et al. 2013). We then calculated the mean eigenvector centrality of all

Figure 2
Boxplots (median, 25% and 75% quartiles, and 95% confidence interval) of the number of proximal encounters for bighorn ewes dyads at Ram Mountain by year (note the $\log_{10}$ scale). The proportion of collared females was 65% in 2011 ($n = 90$ dyads), 63% in 2012 ($n = 132$), and 81% in 2013 ($n = 132$). The number of encounters in 2011 and 2012 was left-skewed with similar frequencies of encounters, whereas in 2013, it was approximately normally distributed and significantly different from 2011 to 2012. Nonoverlapping notches illustrate differences between and among groups (Chambers et al. 1983).

Table 2
Effects of variables on the frequency of proximity events among bighorn sheep ewes at Ram Mountain, 2011–2013

Variable	2011 ($n = 13$) $R^2 = 0.04$	2012 ($n = 17$) $R^2 = 0.08$	2013 ($n = 17$) $R^2 = 0.12$
Relatedness	**Effect: −** **P = 0.03**	Effect: − P = 0.07	Effect: null P = 0.52
Similarity of age	Effect: null P = 0.69	Effect: null P = 0.21	Effect: null P = 0.23
Similarity of dominance rank	Effect: null P = 0.64	Effect: null P = 0.17	Effect: null P = 0.14
Similarity of reproductive status	Effect: null P = 0.94	Effect: null P = 0.10	**Effect: +** **P = 0.03**

Significant effects are emboldened. (+): strong; (−): weak.

individuals for each random network and compared these distributions to the observed network. We considered that observed patterns were not random if they were within the 5% of extremes of the random distribution.

From the observed yearly social networks, we calculated eigenvector centrality and graph strength (Supplementary Tables 1 and 2) for each ewe. Within a framework of multiple competing hypotheses (Johnson and Omland 2004), we tested whether age, dominance rank, and reproductive status (Table 3) better explained why some ewes are more social as measured by their individual eigenvector centrality and graph strength, using generalized linear mixed effect models. Covariates of interest were standardized by their *z*-scores to compare effect sizes. We controlled for year effects as a fixed factor because there were only 3 levels (Bolker et al. 2009). Ewe identity was included as a random variable to control for repeated measures. Parsimony was evaluated using Akaike's information criterion (AIC). We considered any models with ΔAIC <3 to be indistinguishable (Burnham and Anderson 2002). We calculated AIC weights (AIC$_w$), to show the distribution of likelihoods across competing models and Marginal and Conditional R^2 (Nakagawa and Schielzeth 2013) to quantify the variation in centrality explained by each competing model. We averaged all models with ΔAIC <3. We computed mixed models in R v. 2.15 (R Development Core Team 2015) using package Lme4 (Bates and Maechler 2010) and AIC analyses and R^2 analyses using MuMIn (Barton 2010).

RESULTS

The social networks constructed with proximity events differed from random networks generated by simulations. For all 3 years, the mean value of eigenvector centralities was not within the 95% confidence interval of the random networks (Supplementary Figure 1), suggesting that ewes did not associate at random with other ewes in the population.

There was variation in the total number of proximity events per dyad registered in different years (mean [SD]: 451 [327], 288 [230], and 569 [308] from 2011 to 2013, respectively; Figure 2). Despite this variation, Mantel tests suggest that the frequency of association for dyads was correlated between years, suggesting that ewes did consistently associate with specific individuals in consecutive years (2011–2012: $r = 0.38$, $P = 0.04$; 2012–2013: $r = 0.51$, $P < 0.001$).

Results from the multiple regression matrices illustrated that ewes with similar age or similar dominance status did not significantly associate together across all years of the study (Table 2). For relatedness and reproductive status, however, results were inconsistent. In 2011 and 2012, but not in 2013, ewes tended to associate with individuals to which they were less related (Table 2). In 2013, ewes had more proximity events with individuals within their own reproductive class, that is, with or without a lamb at heel; this effect was not detected in 2011 and 2012 (Table 2).

Each yearly network showed variability in strength of association and social structure (Figure 1). For eigenvector centrality, which incorporates both direct and indirect associations, we could not distinguish between the model that included age and the model that included reproductive status; both were more parsimonious than the global model or the model that included social rank (Table 3). Parsimonious models explained between 16% (reproductive status) and 19% (age) of the marginal variance in our data. Age and reproductive status had significant ($P < 0.01$) and negative effects on eigenvector centrality (Table 4).

Table 3

Four competing a priori generalized linear mixed models for explaining eigenvector centrality[a] among bighorn sheep ewes at Ram Mountain, 2011–2013

Variable	ΔAIC	AIC$_w$[b]	Marginal R^{2c}	Conditional R^{2c}	β[d]	P value[e]
Null (year only)	3.13	0.15	<0.01	0.35	—	—
Age	**1.63**	**0.23**	**0.19**	**0.40**	**−0.11**	**0.003**
Rank	4.08	0.07	0.14	0.39	−0.10	0.01
Reproductive status	**0.00**	**0.54**	**0.16**	**0.59**	**−0.20**	**0.001**
Global model	8.17	0.00	0.26	0.62	Age = −0.11 Rank = 0.03 Reproductive status = −0.174	Age = 0.05 Rank = 0.32 Reproductive status = 0.01

For similar analyses with graph strength, see Supplementary Table 1. Each model controls for year as a fixed effect and individual ID as a random effect. Selected models are in bold.
[a]ArcSin Square Root transformed to improve normality of model residuals.
[b]AIC weight.
[c]Nakagawa and Schielzeth (2013).
[d]Nonfactor covariates standardized into z-scores for comparison of effect size.
[e]P value conservatively calculated from t-distribution assuming $n − 1$ degrees of freedom where n is equal to the number of random groups, i.e., 29 unique individuals rather than 59 observations.

Table 4

Model average results from 4 competing a priori generalized linear mixed models for explaining eigenvector centrality among bighorn sheep ewes at Ram Mountain, 2011–2013

Variable	β[a]	P value[b]
Intercept	1.03	**<0.001**
Age	−0.11	**0.004**
Reproductive status	−0.20	**0.002**
Year (2012)	0.05	0.49
Year (2013)	−0.01	0.90

For similar analyses with graph strength, see Supplementary Table 2. Each model controls for year as a fixed effect and individual ID as a random effect. Significant P values in bold.
[a]Nonfactor covariates standardized into z-scores for comparison of effect size.
[b]P value conservatively calculated from t-distribution assuming $n − 1$ degrees of freedom where n is equal to the number of random groups, i.e., 25 unique individuals rather than 47 observations.

Our models investigating the effect of direct associations using graph strength were consistent with those with eigenvector centrality. They were, however, somewhat less clear (Supplementary Table 1). For example, the null model (year) was included in our most parsimonious model set. This model set also included age, rank, and reproductive status (Supplementary Table 1). Models explained between 25% (year) and 35% (age) of the marginal variance in the data. Model-averaged results also indicated negative and significant effects on centrality for age and reproductive status ($P < 0.04$) and an insignificant ($P = 0.10$) negative effect of rank (Supplementary Table 2).

DISCUSSION

Our study suggests that a nonrandom pattern of association among wild ewes is relatively stable across years. However, we found between-year variation in the number of proximity events observed. Commensurate with P_2 and P_4, we observed that age and reproductive status appeared to have an effect, albeit weak, on network centrality but this effect was largely absent for frequency of proximal associations. Contrary to P_3, we found no effect of dominance rank on either proximal associations or network centrality when indirect connections were considered (but see Supplementary Table 1 for

results accounting only for direct connections). We did find weak evidence that related ewes may avoid each other at fine spatial scales, which departs from P_1 where we suggested that related ewes are more likely to associate. It also departs from the null hypothesis, suggesting no difference in proximal association rates for related and unrelated ewes. This result confirms that there is no genetic substructuring in social groups of bighorn ewes (Festa-Bianchet 1991). The strong deviation from random associations in yearly values and the variable interannual stability of social associations, however, suggest that some unidentified variable(s) may drive the patterns of association.

Related ewes did not have stronger social bonds than unrelated ones (P_1). For this population, gregariousness is beneficial (Vander Wal et al. 2015). However, pairwise proximal associations within groups appear independent of kin relationships. Apart from reproductive status (P_4), none of the pairwise predictors of proximal association had significant effects in 2013. We speculate that this pattern, in conjunction with the increase in proximity events in 2013 compared to the previous 2 years (Figure 1), may be attributable to differences in perceived predation risk. In this ecological context associating at finer spatial scales and in nursery groups appear more critical than other cofactors. Indeed, guppies (*Poecilia reticulata*) exposed to higher risk of predation strengthened their social bonds (Kelley et al. 2011).

Indeed, in 2013, we repeatedly saw a cougar (*Puma concolor*) while observing bighorn ewes. Cougar predation on bighorn sheep appears to be due to specialist individuals as most cougars normally prey on cervids (Ross et al. 1997). In 2013, over a third of the ewes disappeared over 12 months. This very high mortality, more than triple the normal rate (Loison et al. 1999), was similar to that seen during earlier episodes of predation by specialist sheep-killing cougars in this population (Festa-Bianchet et al. 2006) and elsewhere (Bourbeau-Lemieux et al. 2011). Since monitoring of this population began in 1971, this is the second time a cougar consistently depredated sheep throughout the summer.

Our results did not support our prediction (P_3) of cohort or familiarity effects (Ehardt and Bernstein 1987). This hypothesis states that individuals of similar age (Pérez-Barbería et al. 2005) will associate frequently because they should be familiar with each other. Instead, preferential associations were not more likely to occur among ewes of similar age or dominance rank. The frequent

trapping regularly dispersed groups, as trapped ewes were released one at a time. Therefore, it is unlikely that associations persisted simply because individuals who got together remained together. Instead, our results suggest that some dyads actively sought each other out, while others appeared to show reciprocal avoidance.

Although the positive effect of similarity of reproductive status on proximal associations was small (c.f. its negative effect on centrality), this result is interesting from a behavioral and adaptive perspective. Nursing ewes experience a trade-off between foraging and vigilance (Rieucau and Martin 2007). Therefore, it might be beneficial to share vigilance with other nursing ewes, while maximizing foraging efficiency, as suggested by the limited attention theory (Griffiths et al. 2004). Vigilance by nursing ewes can increase survival of both mothers and lambs (Rieucau and Martin 2007). Hence, to increase her fitness, a ewe should associate in large groups to benefit from the dilution effect and, at a finer scale, seek conspecifics who share the same trade-off between foraging and vigilance.

Vander Wal et al. (2015) showed fitness benefits for lactating ewes that were more central in social networks based on group membership, that is, networks predicated on the assumption of the gambit-of-the-group (Franks et al. 2009). Here, we report that at a finer spatial scale (<1.5 m) ewe centrality is negatively affected by lactation. This suggests that lambless ewes are more connected to other ewes across reproductive states, leading to no effect of reproductive similarity on frequency of proximal associations (2011, 2012; Table 2). The extent to which these patterns of centrality derived from proximal associations present a fitness advantage remains to be investigated, and because much of the variability in association strength remains unexplained, it seems likely that other variables may override the potential effects of reproductive status.

Younger ewes are more central in social networks, suggesting that gaining social experience early in life may provide fitness benefits. Early-life exposure to more social behaviors increases fitness later in life in cooperatively breeding cichlids (Taborsky et al. 2012), striped mice (*Rhabdomys* sp., Jones et al. 2010), manakins (McDonald 2007), and porpoises (Stanton and Mann 2012). Further investigations may reveal that ewes experiencing a diversity of social situations while young are more likely to exhibit optimal behavioral responses later in life. Interestingly, we found that the determinants of pairwise proximal associations and social centrality were not the same: younger ewes were more central, but age differences had no effect on dyadic associations. As a result, the determinants of costs and benefits of behaviors at the level of the dyad, such as social bond, may differ from those affecting behaviors that emerge at the network level.

We used detailed information on proximity events to evaluate factors affecting the frequency of fine-scale associations and individual differences in social network centrality. Our results suggest that the key factors influencing social centrality in bighorn ewes were age and reproductive status; yet, both had either no effect or an ambiguous effect on frequency of pairwise proximal associations. We speculate that both measures of sociality may be affected by perceived risk of predation. The main benefit of gregariousness for ungulates is predator avoidance (Kie 1999). This generalized antipredator benefit, however, is likely not enhanced by associations with related individuals. In addition, there may not be enough closely related adults in the population to form a group sufficient to maximize antipredator benefits (Festa-Bianchet 1991). We suggest that when social structure in fission–fusion animal societies is primarily shaped by antipredation vigilance, we should not expect an effect of relatedness, as benefits are simply derived from associations with conspecifics. Ultimately, we suggest that studying different levels of social organization (dyad vs. network levels) will lead to a better understanding of the factors shaping animal social structure.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

Handling editor: Nick Royle

REFERENCES

Albon SD, Staines HJ, Guinness FE, Clutton-Brock TH. 1992. Density-dependent changes in the spacing behaviour of female kin in red deer. J Anim Ecol. 61:131–137.

Archie EA, Maldonado JE, Hollister-Smith JA, Poole JH, Moss CJ, Fleischer RC, Alberts SC. 2008. Fine-scale population genetic structure in a fission–fusion society. Mol Ecol. 17:2666–2679.

Archie EA, Morrison TA, Foley CAH, Moss CJ, Alberts SC. 2006. Dominance rank relationships among wild female African elephants, *Loxodonta africana*. Anim Behav. 71:117–127.

Barton K. 2010. MuMIn: multi-model inference. R package, version 0.12.2. Available from: http://r-forge.r-project.org/project/mumin/.

Bates D, Maechler M. 2010. lme4: linear mixed-effects models using S4 classes. R package. Available from: http://r-forge.r-project.org/projects/lme4/.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol. 24:127–135.

Bourbeau-Lemieux A, Festa-Bianchet M, Gaillard JM, Pelletier F. 2011. Predator-driven component Allee effects in a wild ungulate. Ecol Lett. 14:358–363.

Boyland NK, James R, Mlynski DT, Madden JR, Croft DP. 2013. Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance. Behav Ecol Sociobiol. 67:1877–1890.

Brent LJN. 2015. Friends of friends: are indirect connections in social networks important to animal behaviour? Anim Behav. 103:211–222.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic. 2nd ed. New York: Springer.

Cameron EZ, Setsaas TH, Linklater WL. 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc Nat Acad Sci. 106:13850–13853.

Chambers JM, Cleveland WS, Kleiner B, Tukey PA. 1983. Graphical methods for data analysis. New York: Chapman and Hall.

Clutton-Brock T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science. 296:69–72.

Clutton-Brock T, Huchard E. 2013. Social competition and its consequences in female mammals. J Zool. 289:151–171.

Coltman DW, O'Donoghue P, Hogg JT, Festa-Bianchet M. 2005. Selection and genetic (co)variance in bighorn sheep. Evolution. 59:1372–1382.

Costenbader E, Valente TW. 2003. The stability of centrality measures when networks are sampled. Soc Networks. 25:283–307.

Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol. 26:502–507.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research. R package. Available from: http://cran.r-project.org/web/packages/igraph/.

De Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav. 55:827–843.

De Vries H, Netto WJ, Hanegraaf PLH. 1993. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour. 125:157–175.

Ebensperger LA, Rivera DS, Hayes LD. 2012. Direct fitness of group living mammals varies with breeding strategy, climate and fitness estimates. J Anim Ecol. 81:1013–1023.

Ehardt CL, Bernstein IS. 1987. Patterns of affiliation among immature rhesus monkeys (*Macaca mulatta*). Am J Primatol. 13:255–269.

Favre M, Martin JGA, Festa-Bianchet M. 2008. Determinants and life-history consequences of social dominance in bighorn ewes. Anim Behav. 76:1373–1380.

Festa-Bianchet M. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Anim Behav. 42:71–82.

Festa-Bianchet M, Coulson T, Gaillard JM, Hogg JT, Pelletier F. 2006. Stochastic predation events and population persistence in bighorn sheep. Proc Biol Sci. 273:1537–1543.

Franks DW, Ruxton GD, James R. 2009. Sampling animal association networks with the gambit of the group. Behav Ecol Sociobiol. 64:493–503.

Goslee SC, Urban DL. 2007. The ecodist package for dissimilarity-based analysis of ecological data. J Stat Softw. 22:1–19.

Grafen A. 1984. Natural selection, kin selection and group selection. In: Krebs JR, Davies NB, editors. Behavioural ecology: an evolutionary approach. 2nd ed. Oxford: Blackwell. p. 62–84.

Griffiths SW, Brockmark S, Höjesjö J, Johnsson JI. 2004. Coping with divided attention: the advantage of familiarity. Proc Biol Sci. 271:695–699.

Hughes WO, Oldroyd BP, Beekman M, Ratnieks FL. 2008. Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science. 320:1213–1216.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. Trends Ecol Evol. 19:101–108.

Jones MA, Mason G, Pillay N. 2010. Early social experience influences the development of stereotypic behaviour in captive-born striped mice *Rhabdomys*. Appl Anim Behav Sci. 123:70–75.

Jorgenson JT, Festa-Bianchet M, Gaillard J-M, Wishart WD. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. Ecology. 78:1019–1032.

Kelley JL, Morrell LJ, Inskip C, Krause J, Croft DP. 2011. Predation risk shapes social networks in fission-fusion populations. PLoS One. 6:e24280.

Kie JG. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. J Mammal. 80:1114–1129.

Krakauer AH. 2005. Kin selection and cooperative courtship in wild turkeys. Nature. 434:69–72.

Krause J, Wilson ADM, Croft DP. 2011. New technology facilitates the study of social networks. Trends Ecol Evol. 26:5–6.

Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M. 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. Trends Ecol Evol. 29:326–335.

Lichstein JW. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188:117–131.

Loison A, Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology. 80:2539–2554.

Lusseau D. 2003. The emergent properties of a dolphin social network. Proc Biol Sci. 270(Suppl 2):S186–S188.

Lusseau D, Newman ME. 2004. Identifying the role that animals play in their social networks. Proc Biol Sci. 271(Suppl 6):S477–S481.

McDonald DB. 2007. Predicting fate from early connectivity in a social network. Proc Nat Acad Sci. 104:10910–10914.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol. 4:133–142.

Nunez CMV, Adelman JS, Rubenstein DI. 2015. Sociality increases juvenile survival after a catastrophic event in the feral horse (*Equus caballus*). Behav Ecol. 26:138–147.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2013. Package 'vegan'. R Packag Ver. 254:20–28.

Pelletier F, Festa-Bianchet M. 2006. Sexual selection and social rank in bighorn rams. Anim Behav. 71:649–655.

Pérez-Barbería FJ, Robertson E, Gordon IJ. 2005. Are social factors sufficient to explain sexual segregation in ungulates? Anim Behav. 69:827–834.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, de Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, et al. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav Ecol. 25:242–255.

Podgórski T, Scandura M, Jędrzejewska B. 2014. Next of kin next door – philopatry and socio-genetic population structure in wild boar: dispersal and population structure in wild boar. J Zool. 294:190–197.

Poissant J, Réale D, Martin J, Festa-Bianchet M, Coltman D. 2013. A quantitative trait locus analysis of personality in wild bighorn sheep. Ecol Evol. 3:474–481.

Poissant J, Wilson AJ, Festa-Bianchet M, Hogg JT, Coltman DW. 2008. Quantitative genetics and sex-specific selection on sexually dimorphic traits in bighorn sheep. Proc Biol Sci. 275:623–628.

Prange S, Jordan T, Hunter C, Gehrt SD. 2006. New radiocollars for the detection of proximity among individuals. Wildl Soc Bull. 34:1333–1344.

R Development Core Team. 2011. R version 3.0.3. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

R Development Core Team. 2015. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Rieucau G, Martin JGA. 2007. Many eyes or many ewes: vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. Oikos. 117:501–506.

Rioux-Paquette E, Festa-Bianchet M, Coltman DW. 2010. No inbreeding avoidance in an isolated population of bighorn sheep. Anim Behav. 80:865–871.

Ross PI, Jalkotzy MG, Festa-Bianchet M. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Can J Zool. 75:771–775.

Sih A, Hanser SF, McHugh KA. 2009. Social network theory: new insights and issues for behavioral ecologists. Behav Ecol Sociobiol. 63:975–988.

Silk JB. 2002. Using the 'F'-word in primatology. Behaviour. 139:421–446.

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philos Trans R Soc Lond B Biol Sci. 362:539–559.

Smith JE, Memenis SK, Holekamp KE. 2007. Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). Behav Ecol Sociobiol. 61:753–765.

Stanton MA, Mann J. 2012. Early social networks predict survival in wild bottlenose dolphins. PLoS One. 7:e47508.

Taborsky B, Arnold C, Junker J, Tschopp A. 2012. The early social environment affects social competence in a cooperative breeder. Anim Behav. 83:1067–1074.

Vander Wal E, Festa-Bianchet M, Réale D, Coltman DW, Pelletier F. 2015. Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. Ecology. 96:631–641.

Vander Wal E, Paquet PC, Andres JA. 2012. Influence of landscape and social interactions on transmission of disease in a social cervid. Mol Ecol. 21:1271–1282.

Wey T, Blumstein DT, Shen W, Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav. 75:333–344.

Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim Behav. 69:1357–1371.

Wolak ME. 2012. nadiv: an R package to create relatedness matrices for estimating non-additive genetic variances in animal models. Methods Ecol Evol. 3:792–796.