

Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment

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Abstract. The adaptive nature of sociality has long been a central question in ecology and evolution. However, the relative importance of social behavior for fitness, compared to morphology and environment, remains largely unknown. We assessed the importance of sociality for fitness (lamb production and survival) in a population of marked bighorn sheep (*Ovis canadensis*) over 16 years ($n = 1022$ sheep-years). We constructed social networks from observations ($n = 38\,350$) of group membership ($n = 3150$ groups). We then tested whether consistent individual differences in social behavior (centrality) exist and evaluated their relative importance compared to factors known to affect fitness: mass, age, parental effects, and population density. Sheep exhibited consistent individual differences in social centrality. Controlling for maternal carryover effects and age, the positive effect of centrality in a social network on adult female lamb production and survival was equal or greater than the effect of body mass or population density. Social centrality had less effect on male survival and no effect on adult male lamb production or lamb survival. Through its effect on lamb production and survival, sociality in fission–fusion animal societies may ultimately influence population dynamics equally or more than morphological or environmental effects.

Key words: behavioral plasticity; bighorn sheep; centrality; fission–fusion animal societies; fitness; lamb production; *Ovis canadensis*; population dynamics; Ram Mountain Alberta, Canada; sex-based differences; sociality; survival.

INTRODUCTION

Theory predicts that social behaviors, including pairwise associations, will evolve if they result in a net lifetime benefit through increased fecundity or survival (Silk 2007a, Ebensperger et al. 2012). Many studies, however, have failed to detect fitness benefits of social behaviors. For example, 58% of studies on group-living in mammals found no effect (Ebensperger et al. 2012), suggesting that sociality generally has a weak effect on fitness (Ebensperger et al. 2012). Furthermore, very few studies have compared the fitness consequences of sociality to those of other critical variables, such as population density, body mass, or age. Thus, it is important to both determine if social behavior in the wild is adaptive and rank its importance for explaining differences in fitness.

Studies of social behavior directly affecting individual fitness are rare (reviews in Silk 2007a, Ebensperger et al. 2012), and most have involved one or two years of

monitoring a segment of the population. However, the contribution of social behaviors to fitness has been well studied in cooperative breeders, e.g., *Canis* spp. (Stahler et al. 2012), *Suricata suricatta* (Clutton-Brock et al. 2001), and *Marmota* spp. (Armitage and Schwartz 2000). In cooperative breeders, groups are often kin-based and fitness benefits are attributed to inclusive fitness (Jennions and Macdonald 1994). The benefits of social behavior are less clear for social mammals that are neither plural breeders with communal care nor cooperative breeders. A recent meta-analysis (Ebensperger et al. 2012) found no effect of group-living on fitness for these types of social organization. A few notable examples, however, do exist. For instance, social behaviors, such as stable social bonds, improve infant survival (Silk et al. 2003) and adult longevity (Silk et al. 2010) in baboons *Papio cynocephalus* (see Silk 2007b for review), and foal production among unrelated feral mares *Equus caballus* (Cameron et al. 2009).

The latter examples involve animal societies with relatively stable social groups. Many social mammals, however, exhibit fission–fusion (Aureli et al. 2008, Haydon et al. 2008), where social bonds often appear to be ephemeral and are challenging to quantify. Nevertheless, these possibly subtle and dynamic social

Manuscript received 8 July 2014; accepted 24 July 2014.
Corresponding Editor: C. C. Wilmsers.

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behaviors can create intricate networks of relationships (Croft et al. 2011), similar to a physical landscape. These networks contain complex multi-scale social structure (Couzin 2006). Few studies have tested whether individual- or higher-order social network structures are adaptive (but see Lea et al. 2010). None has tested fission–fusion societies, despite their abundance in nature. If social behaviors in fission–fusion societies affect fitness, a signal should be detected within the architecture of the social network. This signal, however, may differ by sex and fitness component. In sexually dimorphic species that exhibit sexual segregation, sociality may have differential costs and benefits.

We investigated how variability in social behavior at multiple scales can affect the components of fitness (lamb production and survival), using a 16-year (1996–2011) bighorn sheep (*Ovis canadensis*) data set. Specifically, we compared the relative importance of social behavior against morphology and density, two factors known to strongly affect lamb production and survival. The data included complete life histories for >99% of the population (Gaillard et al. 2000), with observations of individual group memberships. From these data, we constructed yearly social networks (Croft et al. 2011) and extracted multi-scale indicators of social behavior. We first tested whether individual-based network measures of centrality are repeatable within each individual and whether differences exist among individuals. This is critical for understanding the potential for selection on behavior. For females, we further tested whether changes in social centrality are consistent across reproductive states, because lactating females may form nursery groups, increasing centrality. Following this, we treated our two central questions. (1) Can sociality affect sex-specific lamb production and survival? Most importantly, (2) if sociality affects fitness, where does its importance rank compared to morphological and environmental factors?

METHODS

Bighorn sheep and study area

Bighorn sheep are social ungulates. Female primiparity is typically at three years (Martin and Festa-Bianchet 2011a). Breeding females produce one offspring per year. Age and body mass are known to increase lamb production, lamb survival, and adult survival (Festa-Bianchet et al. 1998). Bighorn sheep form fission–fusion groups and there is no evidence that groups are kin-based (Festa-Bianchet 1991). Groups can sort by body mass, and young males leave female groups between the ages of two and three years to join bachelor groups (Ruckstuhl and Festa-Bianchet 2001). Adults typically segregate sexually outside the rut (Ruckstuhl and Neuhaus 2002). Dominance is generally correlated with age and body mass (Pelletier and Festa-Bianchet 2006, Favre et al. 2008). Dominant males exhibit female defense polygyny and subordinate males may adopt a courting strategy (Hogg 1984). Paternity is skewed

toward a few dominant individuals (Coltman et al. 2002).

The bighorn sheep of Ram Mountain, Alberta, Canada (52° N, 115° W) have been continuously monitored since 1972 (Jorgenson et al. 1993). Here, we used data collected between 1996 and 2011 ($n = 38\,350$ observations, 3150 groups, 1022 sheep-years), when group composition was available. During this period, the population fluctuated from 188 to 42 individuals. Between May and September, animals were baited with salt into a corral trap where they were weighed (kg) and fitted with colored collars or plastic ear tags (Jorgenson et al. 1993). Maternity was assigned by visual observations of suckling. Lamb production was scored by observing a mother with a lamb following parturition (Festa-Bianchet 1988). Survival was calculated as survival of marked individuals at time t and resighted in the subsequent capture season ($t + 1$). Paternity was assigned using data from genotyped microsatellite loci (for details, see Coltman et al. 2002). From 1997 to 2001, there was substantial predation during the capture season (Réale and Festa-Bianchet 2003); the role of predation outside of the capture season is unknown.

Group observations

Between mid-May and September 1996–2011, field crews sought out groups of bighorn sheep (see Plate 1). Ram Mountain is a small area (~28 km²) where sheep are mostly found in rocky slopes, cliffs, and alpine meadows. There is no evidence that the population is structured in space. Group size was relatively constant throughout the sampling season: 21 ± 6 females (mean ± SD); 19 ± 7 males. Groups were frequently located multiple times per week, and multiple groups per day were often observed. The identity of each individual in each group was recorded. Unlike many other ungulates, bighorn sheep form discrete and easily quantifiable groups. Groups involved all individuals that could conceivably associate in a pairwise fashion. Typically, individuals at the peripheries of groups were no more than 100 m apart. In the infrequent circumstances when designating a group was unclear, crews continued to observe groups, for at least 1 hour, to ascertain if fusion occurred. Given the restricted range of the sheep population, each animal was regularly resighted: 37 ± 20 resightings/yr per individual female (mean ± SD); 22 ± 18 resightings/yr per individual male. It is very uncommon for adults in this population to die in the summer, so individuals were relocated throughout the sampling season.

Network analyses

Networks consisted of all pairwise combinations of animals in a group. For each dyad throughout each field season, we calculated a half-weight index [HWI, (Cairns and Schwager 1987)], accounting for unequal probability of detection and uneven sampling. We constructed networks weighted by the HWI using the iGraph



PLATE 1. A mixed group of bighorn sheep. Photo credit: Gabriel Pigeon.

package (Csardi and Nepusz 2006) in R (R Development Core Team 2011) for each year. Bighorn sheep generally segregate into size-specific (and therefore sex-specific) groups. Therefore, one network included all females, and yearling and two-year-old males. At two years of age, males may be large enough to transition into male groups and were therefore also included in the second network, which included all males ≥ 2 years old (Ruckstuhl and Neuhaus 2005). Because lambs depend on their mothers until weaning, networks only included individuals that were ≥ 1 year old.

We calculated two principle measures on unfiltered networks (Lusseau et al. 2008): eigenvector centrality (individual sociality) and graph density. We chose eigenvector centrality (EC) as our primary measure of centrality because it efficiently approximates centrality in a network by accounting for direct and indirect associations (Costenbader and Valente 2003, Maiya and Berger-Wolf 2010), and has been shown to be effective in other studies (e.g., Aplin et al. 2012, Stanton and Mann 2012). We chose a single metric over principal components of multiple correlated network metrics (Wey and Blumstein 2012) to simplify our hypothesis set. Eigenvector centrality of each individual is proportional to the sum of the centralities of individuals to which it is connected (i.e., observed in the same group). In general, individuals with high eigenvector centralities are connected to many other individuals that are, in turn, connected to many individuals (Csardi and Nepusz

2006). Further details on eigenvector centrality are provided in Appendix A.

For comparison, in addition to EC, we replicated all analyses using a simpler metric: graph strength. Graph strength is the sum of all weighted edges of a node (Csardi and Nepusz 2006) and does not account for indirect ties among individuals. Graph strength was correlated to eigenvector centrality ($R^2 = 0.97$ and 0.80 for females and males, respectively) and all model results remained consistent between the two indicators of centrality. All results of replicated analyses for graph strength are in Appendix B: Tables B1 and B2.

We consider EC an individual-level network metric because it quantifies an individual's centrality and varies among nodes within the network. Graph density (GD) is the proportion of edges present in a population in relation to the number of possible edges (Csardi and Nepusz 2006). Edges are absent in this population-level network metric only when two individuals have never been observed in the same group. As such, GD is invariant across nodes within a network and is therefore a population-level property.

Repeatability and behavioral reaction norms

To determine whether consistent individual differences in social centrality were present across age classes over time, we calculated repeatability using the interclass correlation coefficient (ICC). The ICC partitions the proportion of among-individual to within-individual

TABLE 1. Competing models to explain variation in different measures of fitness (lamb production, lamb and adult survival) in bighorn sheep (*Ovis canadensis*) on Ram Mountain, Alberta, Canada.

Hypothesis	Centrality	Graph density (GD)	Parent mass	Maternal effects (ME)	Age (+age ²) [†]	Population density (N)
H_{1a}	X					
H_{1b}		X				
H_{1c}	X	X				
H_2			X		X	
H_3			X	X	X	
H_4						X
H_5		X	X	X	X	X
H_6	X	X	X	X	X	X

Notes: H_1 includes three social models: individual-level effects (a), population-level effects (b), and both with their interaction (c). Alternate hypotheses include: morphology (H_2); morphology and maternal effects (H_3); population density only (H_4); morphology, maternal effects, and density (H_5); and the global model (H_6).

[†] The spline of age (age²).

variation on a scale of 0 to 1. Highly repeatable behaviors have values near 1; behaviors that are not repeatable are not significantly different from 0. For EC, we calculated repeatability using the R package MCMCglmm to ensure reliable estimates of 95% credible intervals (Hadfield 2010).

We calculated behavioral reactions norms (Dingemanse et al. 2010) for females, to ascertain that centrality was exclusively dependent on reproductive status (with and without lamb) or whether centrality was selection based. To calculate reaction norms and test for an interaction between individuals and state, we used mixed general linear models for females ≥ 3 years old following Martin et al. (2011). Furthermore, we calculated Kendall's tau to test the correlation between an individual's EC in years with and years without offspring at heel.

General linear models

All variables were converted to z scores and screened for excessive correlations ($r > 0.7$) and collinearity (variance inflation factor, VIF > 10 ; Dormann et al. 2013). All models controlled for two random effects: sheep identity (ID) to account for dyadic autocorrelation of network measures, and year. We used generalized linear mixed models (GLMMs) for binomial response variables for lamb production and survival using the lme4 package (Bates and Maechler 2010) in R. Males were divided into two categories: those that sired at least one offspring and those that did not. Because all individuals were marked at birth, their age was known. Individual sheep were repeatedly captured each year and weighed. Linear regressions were used to adjust individual mass to 15 September each year (Martin and Festa-Bianchet 2011b). Population density was calculated by a census of all individuals within the sample season. The population density in the year of birth of each ewe was used as a proxy for maternal effects in all models except male lamb production.

Hypotheses, model selection, and variable rank

We employed a multiple competing hypotheses (Johnson and Omland 2004) approach within an information theoretic framework (Burnham and Anderson 2002) to test six hypotheses. The six hypotheses fell into three families: social, morphological, and environmental (Table 1). We hypothesized (H_{1a}) that being more central in a network will positively affect fitness; that fitness will increase with increased associations among members of a population (H_{1b}); and that both individual-level (EC) and population-level (GD) measures of sociality and their interaction will positively affect fitness (H_{1c}). These hypotheses competed against alternate models, which include measures of mass and age (morphological, H_2 and H_3); influence of maternal carryover effects (morphological, H_3 ; and morphological-environmental, H_5); and population density (environmental, H_4). Mass, age, and density all affect fitness in general and specifically in this population (Festa-Bianchet et al. 1998). Finally, we tested a model including all covariates (H_6).

We used information criteria to first distinguish between fit and parsimony of candidate models H_1 – H_6 (Burnham 2002). For GLMMs, we used Akaike's information criteria (AIC). We adopted a liberal approach and considered any models with $\Delta AIC < 3$ to be indistinguishable. Furthermore, for GLMMs, we ranked variable importance using an all-possible-models approach (Murtaugh 2009). For each GLMM, we constructed a model with all variables in the most parsimonious candidate models, H_1 – H_6 . We ran models on all possible combinations of covariates, i.e., for n covariates, 2^n possible models were compared. This typically produces a new subset of most parsimonious models. Our approach here was more conservative, and we only selected models with $\Delta AIC < 2$. Each model was assigned an Akaike weight (AIC_w), the probability that each model is the most parsimonious. Subsequently, the most parsimonious models were averaged to

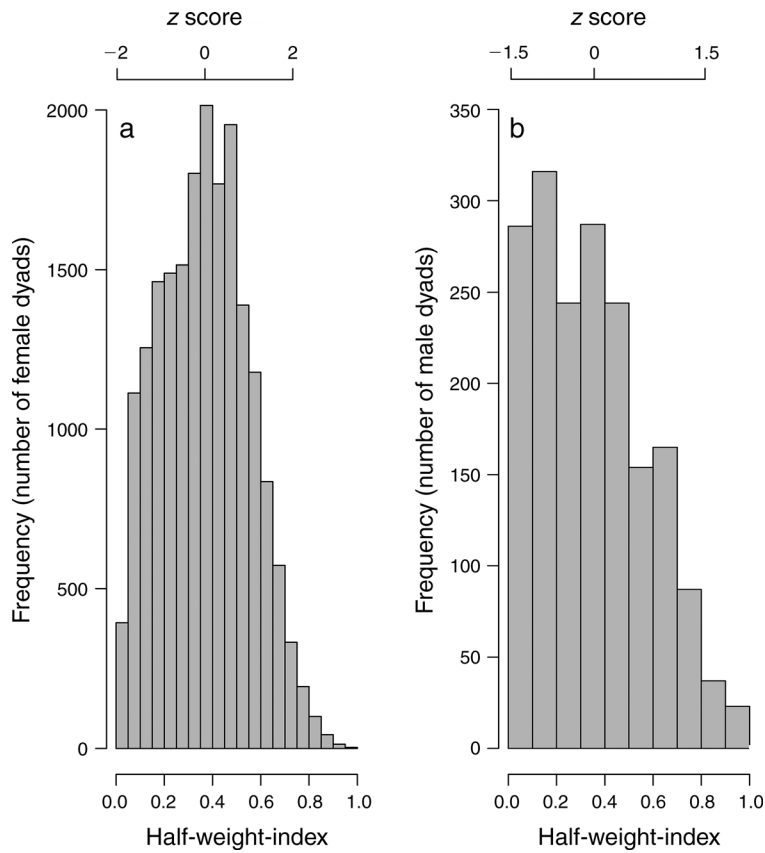


FIG. 1. Distribution of pairwise association strengths according to the half-weight index and corresponding z-score, derived from gambit-of-the-group data from a fission–fusion society of (a) female ($n = 18\,157$) and (b) male ($n = 18\,43$) bighorn sheep (*Ovis canadensis*) on Ram Mountain, Alberta, Canada, 1996–2011. Networks consisted of all pairwise combinations (dyads) of animals in a group. For each dyad throughout each field season, we calculated a half-weight index (Cairns and Schwager 1987), accounting for unequal probability of detection and uneven sampling. One network (a) included all females plus yearling and two-year-old males; the second network (b) included all males ≥ 2 years old. For details, see *Methods: Network sampling*.

calculate averaged β coefficients and unconditional standard errors. From here we ranked variable importance. For each independent variable we summed AIC_w for the candidate models in which it occurred with $\Delta AIC < 2$. Thus, variables with $\sum AIC_w = 1.0$ occurred in all parsimonious candidates; $\sum AIC_w = 0.5$ were those variables that occurred only in a subset of parsimonious models whose AIC_w sums to 0.5. We used R package MuMIn to run model averages and calculate variable importance (Barton 2010).

RESULTS

The HWI varied among dyads: 0.37 ± 0.18 (mean \pm SD) for females; 0.36 ± 0.22 for males (Fig. 1). Individual differences in eigenvector centrality were consistent and repeatable: for females, mean $r = 0.40$, 95% CI (credible interval) = 0.32–0.50; for males, mean $r = 0.26$, 95% CI = 0.13–0.42. Although at the population level there was no difference in mean individual centrality between females with and without offspring (Fig. 2a), there was individual plasticity, including a significant individual \times reproductive state

effect ($P < 0.001$; Fig. 2b; Kendall's tau = 0.31, $P < 0.001$).

All models of fitness supported the inclusion of individual-level sociality measured by EC; predominantly this was based on its inclusion in the global model ($\Delta AIC < 3$, Table 2; see Appendix B for replicated results for graph strength). For females, global models explained 19–45% of the variance (Table 2; Appendix B: Table B1). Being more central in the female networks did not affect lamb survival ($P > 0.05$, $AIC_w = 0.13$). Rather, mass and population density were more important (Figs. 3 and 4; $P < 0.01$, $AIC_w = 1$; Table 3; Appendix B: Table B2). However, centrality had a significant ($P < 0.05$) and important ($AIC_w = 1$) positive effect on adult lamb production ($\beta = 0.32$) and adult survival ($\beta = 1.03$; Figs. 3 and 4, Table 3; Appendix B: Table B2). Centrality was as important as mass and population density ($P < 0.05$, $AIC_w = 1.0$; Table 3; Appendix B: Table B2).

For males, sociality was also retained in global models (Table 2; Appendix B: Table B1), which explained 29%–62% of the variance (Table 2; Appendix B: Table B1).

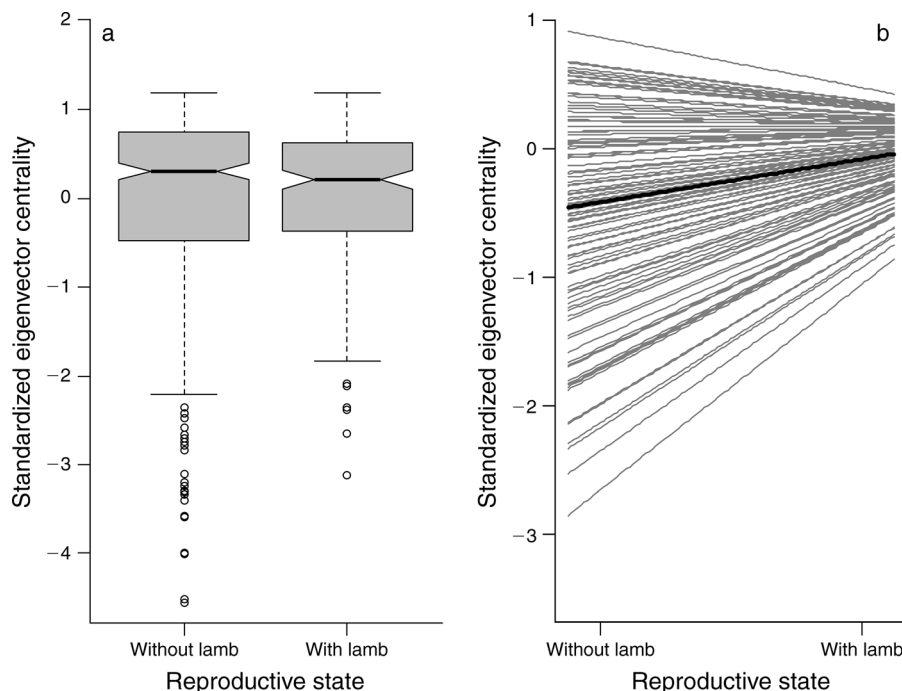


FIG. 2. (a) Population-scale boxplots of median, 25% and 75% quartiles, 95% confidence intervals (“whiskers”), and outlier points of eigenvector centrality for female bighorn sheep without a lamb ($n = 235$ females) and with a lamb ($n = 206$ females). Nonoverlapping notches ($> <$) indicate groups not significantly ($P > 0.05$) different (Chambers et al. 1983). However, individual scale variation does exist; as shown in panel (b): reaction norms illustrating individual plasticity in eigenvector centrality (gray lines) and an individual \times reproductive state effect ($P < 0.001$). The black line indicates the population mean ($n = 111$ females).

Increased centrality ($\beta = 0.12$) was equivocal ($P > 0.05$) and marginally unimportant for male lamb production ($AIC_w = 0.44$; Figs. 3 and 4, Table 4). In contrast, mass ($\beta = 2.60$) was significant and important in all male models of lamb production ($P < 0.05$, $AIC_w = 1.0$; Fig. 4, Table 4). Centrality had no effect on the survival of male lambs ($P > 0.05$, $AIC_w < 0.53$; Table 4; Appendix B: Table B2); rather, population density had the largest effect ($\beta < -0.70$, $P < 0.05$, $AIC_w = 0.85$; Table 4; Appendix B: Table B2). Conversely, population density did not affect adult male survival ($AIC_w = 0$, Table 4;

Appendix B: Table B2). Here centrality had an equivocal but positive effect ($\beta > 0.22$; Fig. 2), more important than mass ($AIC_w = 0.81$ and 0.38 , respectively) but less important than maternal effects ($AIC_w = 1$; Table 4; Appendix B: Table B2).

The influence of social behaviors at the population level was largely equivocal ($P < 0.05$) and unimportant ($AIC_w < 1.0$; Fig. 4). The notable exception was female lamb production ($\beta > 0.40$, $P < 0.05$, $AIC_w = 1.0$; Fig. 4, Table 3). Years when networks had high graph density (i.e., were more connected, typically at lower densities;

TABLE 2. Results for competing models to explain variation in different measures of fitness (lamb production and survival) in bighorn sheep on Ram Mountain, Alberta, Canada.

Hypothesis	Lamb production				Lamb survival				Adult survival (>1 yr)			
	Female ($n = 556$ animal-years, 147 individuals)		Male ($n = 353$ animal-years, 138 individuals)		Female ($n = 96$)		Male ($n = 113$)		Female ($n = 557$ animal-years, 144 individuals)		Male ($n = 227$ animal-years, 87 individuals)	
	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2
H_{1a}	190.97	0.04	104.73	0.28	2.64	0.07	3.39	0.12	17.24	0.28	29.90	0.37
H_{1b}	187.94	0.05	104.51	0.28	2.93	0.07	1.95	0.14	101.43	0.07	30.50	0.36
H_{1c}	183.24	0.07	106.33	0.29	4.06	0.08	1.36	0.19	18.95	0.28	33.62	0.37
H_2	23.45	0.39	11.15	0.56	3.45	0.11	3.94	0.16	82.65	0.13	29.26	0.38
H_3	13.09	0.41	NA	NA	2.87	0.14	3.97	0.18	80.16	0.14	0.00	0.51
H_4	191.58	0.04	163.24	0.06	0.00	0.1	1.67	0.14	118.88	0.02	107.01	0.04
H_5	14.56	0.41	0.00	0.6	2.18	0.18	0.00	0.24	81.99	0.14	1.98	0.51
H_6	0.00	0.45	1.40	0.61	5.08	0.19	1.00	0.29	0.00	0.35	0.33	0.54

Notes: Models were constructed with eigenvector centrality; for results using graph strength, see Appendix B: Table B2. Boldface values represent models with $\Delta AIC \leq 3$ from the best model; NA indicates not applicable.

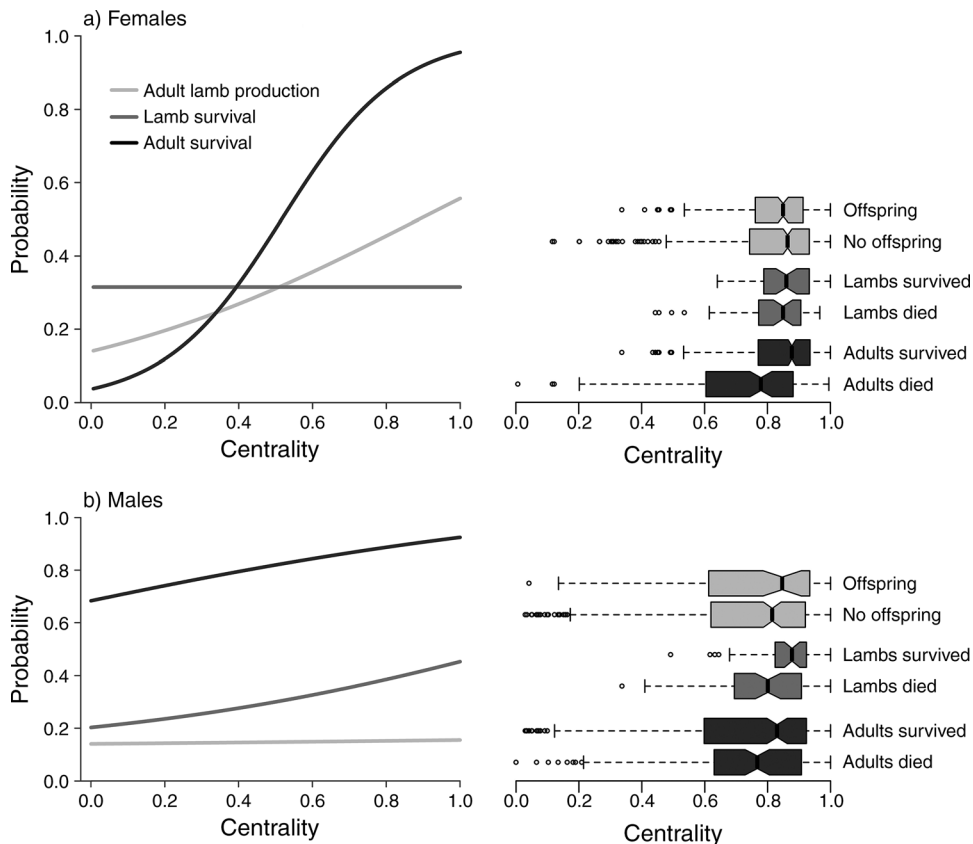


FIG. 3. Fitness component curves and range of the data in boxplots for (a) female and (b) male bighorn sheep at Ram Mountain, Alberta, Canada, depicting individual-level effects on lamb production, lamb survival, and adult survival derived from global models (H_6 , Table 3). Centrality primarily affected adult female lamb production and survival with less influence on lamb survival. Effects were stronger for females (upper) than males (lower). (b) Range of the data in boxplots (median, 25% and 75% quartiles and 95% confidence intervals). Nonoverlapping notches ($> <$) illustrate significant ($P > 0.05$) differences between groups (Chambers et al. 1983) that succeed (in reproducing or surviving) and those that failed.

Appendix C: Fig. C1) had individual-level effects on female lamb production. Moreover, a significant and important negative interaction existed between individual centrality and graph strength ($\beta = -0.37$, $P < 0.05$, $AIC_w = 1.0$; Table 3).

DISCUSSION

Using 16 years of detailed behavioral data on an entire population of marked wild bighorn sheep, our study is one of the first to assess the importance of sociality in a fission–fusion society. We illustrated that social centrality is a consistent, repeatable behavior. Individuals, however, exhibit some plasticity in social centrality, whose expression can be constrained by reproductive state (Dingemanse et al. 2010). Centrality is therefore a behavior upon which selection can act through differential effects on fitness (Réale et al. 2010). Indeed, measures of fitness covaried with sociality. Compared to morphology and environment, factors known to affect fitness, centrality unequivocally ranked equally or more important in two of six scenarios: female adult survival and female lamb production. The

influence of centrality on female lamb production, however, was modified by our population-level index of social connectivity (graph density). Therefore, we argue that female bighorn sheep adopt a social strategy that increases fitness. Social centrality ranked more important for survival than morphology (H_2 and H_3) or environment (H_4) for both sexes. Conversely, lamb survival was unaffected by maternal centrality. In lambs, environment (density) was the strongest driver of mortality.

Unlike plural breeders with communal care or cooperative breeders (Lea et al. 2010, Stahler et al. 2012), bighorn sheep do not form discrete kin-structured groups (Festa-Bianchet 1991). Thus, kin selection is unlikely to explain the evolution of sociality in this species. Yet, social behaviors appear to accord direct fitness benefits primarily through adult female survival and lamb production. Sociality has been observed to affect offspring production in species with stable social structures, e.g., feral horses (Cameron et al. 2009). Similarly, social bonds may affect offspring survival, e.g., in baboons (Silk et al. 2003) and feral horses

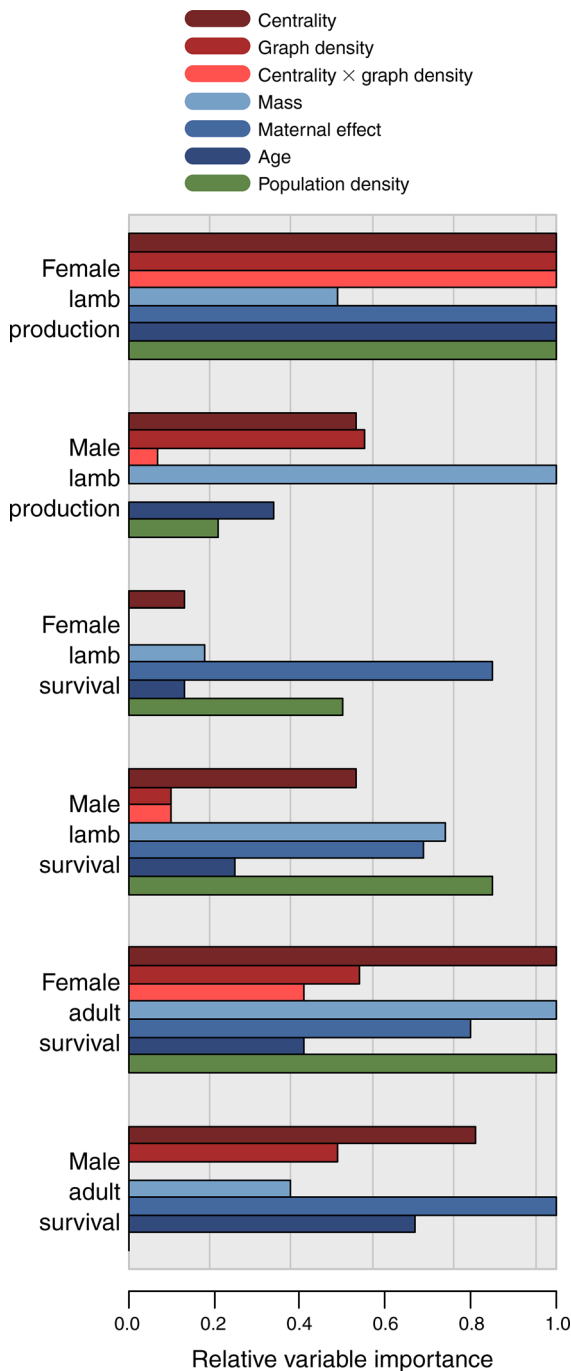


FIG. 4. Relative importance of variables (AIC_w) from three competing families for models: social (red), morphological (blue), and environmental (green), by sex-specific component of fitness (female and male, lamb production, lamb and adult survival). For example, values of 1 suggest that the variable was present in all models with $\Delta AIC < 2$, whereas values of 0.5 indicate that the variable was present in a subset of models where AIC_w summed to 0.5. Variables that are absent were dropped during AIC model selection due to unimportance.

(Cameron et al. 2009). Here, we also observed effects on lamb production, with body mass and maternal effects being equally important. There was no effect, however, on lamb survival, for which population density was more important. Cameron et al. (2009) postulate that fitness benefits in feral horses were accrued through reduced male harassment. This is an unlikely explanation for bighorn sheep, where males do not harass females outside the breeding season (Ruckstuhl and Neuhaus 2002).

For both sexes, centrality improved survival. Previous research linked centrality to adult longevity, e.g., for baboons, (Silk 2007a, Silk et al. 2010) and rock hyrax *Procapra capensis*, (Barocas et al. 2011); and to survival or mortality, e.g., for humans *Homo sapiens* (Holt-

TABLE 3. Model-averaged results from the global model (Table 3) to explain the variation in different measures of fitness in female bighorn sheep on Ram Mountain, Alberta, Canada.

Female fitness component and fixed effects	β	SE	z	P	AIC_w
Lamb production ($n = 556$ animal-years, 147 individuals)					
Intercept	-0.15	0.34	0.46	0.648	NA
Eigenvector centrality	0.32	0.16	2.05	0.040	1.00
Graph density	0.40	0.17	2.30	0.021	1.00
Centrality × graph density	-0.37	0.15	2.50	0.012	1.00
Mass	0.56	0.39	1.43	0.154	0.49
Maternal effect	-0.74	0.18	4.20	< 0.001	1.00
Age	3.04	0.45	6.71	< 0.001	1.00
Age ²	-1.23	0.19	6.57	< 0.001	1.00
Population density	0.73	0.24	3.10	0.002	1.00
Lamb survival ($n = 96$)					
Intercept	-0.41	0.55	0.74	0.458	NA
Eigenvector centrality	0.31	0.32	0.98	0.328	0.13
Graph density†					
Centrality × graph density†					
Mass	0.68	0.83	0.83	0.409	0.18
Maternal effect	-0.45	0.22	2.05	0.040	0.85
Age	0.26	0.34	0.77	0.442	0.13
Age ²	0.21	0.18	1.14	0.255	0.23
Population density	-0.49	0.3	1.64	0.100	0.50
Adult survival ($n = 557$ animal-years, 144 individuals)					
Intercept	2.23	0.28	7.97	< 0.001	NA
Eigenvector centrality	1.03	0.15	6.92	< 0.001	1.00
Graph density	0.03	0.17	0.21	0.836	0.54
Centrality × graph density	-0.20	0.12	1.66	0.097	0.41
Mass	0.82	0.32	2.59	0.010	1.00
Maternal effect	-0.28	0.15	1.94	0.053	0.80
Age	-0.59	0.17	3.42	0.001	0.41
Age ²	-0.22	0.06	3.44	0.001	0.59
Population density	0.58	0.20	2.91	0.004	1.00

Notes: Models were constructed with eigenvector centrality; for results using graph strength, see Appendix C: Table C3. We standardized all variable to their z scores prior to analysis. Boldfaced values report either $P < 0.05$ or relative importance values (AIC_w) = 1; NA indicates not applicable.

† Variable dropped during “all-possible-model” selection.

TABLE 4. Model-averaged results from the global model (Table 3) to explain the variation in different measures of fitness in male bighorn sheep on Ram Mountain, Alberta, Canada.

Male fitness component and fixed effects	β	SE	z	P	AIC _w
Lamb production ($n = 353$ animal-years, 138 individuals)					
Intercept	-3.71	0.73	5.09	<0.001	NA
Eigenvector centrality	0.12	0.23	0.50	0.616	0.44
Graph density	0.27	0.33	0.83	0.409	0.79
Centrality \times graph density	0.28	0.16	1.77	0.076	0.23
Mass	2.60	0.43	5.99	< 0.001	1.00
Age	-0.11	0.33	0.33	0.744	0.08
Age ²	-0.04	0.09	0.43	0.670	0.09
Population density	-0.74	0.40	1.82	0.068	0.73
Lamb survival ($n = 113$)					
Intercept	-1.37	0.51	2.71	0.007	NA
Eigenvector centrality	0.43	0.29	1.49	0.137	0.53
Graph density	0.25	0.33	0.76	0.445	0.10
Centrality \times graph density	-0.56	0.35	1.62	0.106	0.10
Mass	0.44	0.25	1.78	0.075	0.74
Maternal effect	-0.37	0.21	1.76	0.078	0.69
Age	-0.18	0.58	0.31	0.753	0.25
Age ²	0.31	0.20	1.59	0.113	0.67
Population density	-0.70	0.34	2.09	0.037	0.85
Adult survival ($n = 227$ animal-years, 87 individuals)					
Intercept	1.87	0.34	5.57	<0.001	NA
Eigenvector centrality	0.22	0.17	1.31	0.189	0.81
Graph density	-0.2	0.25	0.77	0.439	0.49
Centrality \times graph density†					
Mass	0.81	0.49	1.65	0.100	0.38
Maternal effect	-0.27	0.2	1.36	0.174	1.00
Age	-0.80	0.44	1.83	0.068	0.67
Age ²	-0.20	0.10	2.10	0.036	0.40
Population density†					

Notes: Models were constructed with eigenvector centrality; for results using graph strength, see Appendix C: Table C3. We standardized all variable to their z scores prior to analysis. Boldfaced numbers report either $P < 0.05$ or relative variable importance values (AIC_w) = 1; NA indicates not applicable. † Variable dropped during “all-possible-model” selection.

Lunstad et al. 2010). In some instances, early-life pairwise bonds form network connections that can predict future survival, e.g., in Long-tailed Manakins *Chiroxiphia linearis* (McDonald 2007) and bottlenose dolphins *Tursiops* sp. (Stanton and Mann 2012). In bighorn sheep, however, an individual’s current centrality predicts survival in females and to a lesser extent in males. These results were consistent for centrality as a function of indirect associations (eigenvector centrality) and direct associations (graph strength; Appendix B: Tables B1 and B2).

Using a network approach, we were able to investigate network metrics that represent different scales of social behavior: variable individual centrality, and population-scale graph density. For example, for bighorn ewes, we have presented empirical evidence that

population-scale sociality (the cumulative sum of all individual associations) has positive effects on lamb production. Moreover, this effect is most pronounced when social connectivity in the population is low. Variability in graph density was partially explained by population density (Appendix C: Fig. C1); however, no significant interactive effects between population density and centrality were found (data not shown). Our results from graph density lend some empirical support to the assertion that fitness effects can accrue at the population level and filter down to the individual (Dunbar and Shultz 2007). Ultimately this behavior is driven by associating with a group; here, the ways in which other group members associate within the population appear to also affect individual fitness. One possibility for this multilevel effect is the role of familiarity, i.e., whether individuals are known to one another. Indeed, when the population was well connected, the importance of centrality was lessened. For example, familiarity with conspecifics may decrease the time spent being vigilant or reinforcing hierarchies. According to limited attention theory (Dukas 2002) and the time constraint hypothesis (Dunbar et al. 2009), individuals can only attend to a finite number of relationships at one time (Griffiths et al. 2004). Increased levels of familiarity that accrue at the population level (i.e., higher graph density) in animal societies may reduce the need for individual-level conspecific vigilance. The result is increased “free” time that can be allocated to alternate behaviors, some of which may have positive effects on neighbors, e.g., antipredator vigilance (Roberts 1996). Alternately, increased familiarity may also lead to increased foraging efficiency (Strodl and Schausberger 2012a) and social information on feeding sites (Aplin et al. 2012), and ultimately may increase fitness (König 1994, Strodl and Schausberger 2012b).

Although the mechanism for why social centrality and connectedness accords fitness benefits in bighorn sheep remains unknown, our results support the general understanding of animal societies. Individuals that are well integrated in societies (e.g., baboons; Silk et al. 2003, Silk 2007a), familiar with their neighbors (e.g., Great Tits *Parus major*; Grabowska-Zhang et al. 2011), and nested centrally within the densest substructures of the population reap the highest fitness benefits. Those at the periphery may exhibit marginal gains from social behaviors compared to costs. For example, costs of predation (Beauchamp 2010) may be greater than costs related to acquiring pathogens, which may increase with centrality (Cross et al. 2004). Similarly, costs of competition for resources may be offset by highly social subgroups finding and preferentially accessing prime forage (Rieucan and Giraldeau 2011, Aplin et al. 2012).

Here we highlight the importance, repeatability, and plasticity of social centrality in fission–fusion societies in the wild. How one becomes central in a population remains to be tested as a function of gregariousness or variation in pairwise associations. Nevertheless, varia-

tion in centrality has implications for fitness in bighorn sheep, predominantly affecting adult female lamb production and adult survival. That fitness varies with social behaviors that are consistently expressed throughout life results in the prerequisite variation upon which natural selection acts. As individual sociality has been shown to be heritable in some populations (Frere et al. 2010, Lea et al. 2010), social behavioral differences may play a key role in the fundamental processes of birth and death, and ultimately may affect population and evolutionary dynamics.

ACKNOWLEDGMENTS

The Ram Mountain project has been supported for 40 years by the Alberta Department of Fish and Wildlife and for 23 years by the Natural Science and Engineering Research Council of Canada (Discovery Grants to M. Festa-Bianchet, D. Réale, D. W. Coltman, and F. Pelletier; Post-Doctoral Fellowship to E. Vander Wal). Further financial support was provided by the Alberta Conservation Association and the Canada Research Chair in Evolutionary Demography and Conservation to F. Pelletier. Research has been strongly supported by Jon Jorgenson. We thank all the students and assistants who trapped, measured, and observed sheep throughout the years. The manuscript was markedly improved thanks to comments from two anonymous reviewers and the associate editor.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-1320.1.sm>