



Original Article

# Group social structure has limited impact on reproductive success in a wild mammal

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The frequency and type of dyadic social interactions individuals partake in has important fitness consequences. Social network analysis is an effective tool to quantify the complexity and consequences of these behaviors on the individual level. Less work has used social networks to quantify the social structure—specific attributes of the pattern of all social interactions in a network—of animal social groups, and its fitness consequences for those individuals who comprise the group. We studied the association between social structure, quantified via five network measures, and annual reproductive success in wild, free-living female yellow-bellied marmots (*Marmota flaviventris*). We quantified reproductive success in two ways: (1) if an individual successfully weaned a litter and (2) how many pups were weaned. Networks were constructed from 38 968 interactions between 726 unique individuals in 137 social groups across 19 years. Using generalized linear mixed models, we found largely no relationship between either measure of reproductive success and social structure. We found a modest relationship that females residing in more fragmentable social groups (i.e., groups breakable into two or more separate groups of two or more individuals) weaned larger litters. Prior work showed that yellow-bellied marmots residing in more fragmentable groups gained body mass faster—another important fitness correlate. Interestingly, we found no strong relationships between other attributes of social group structure, suggesting that in this facultatively social mammal, the position of individuals within their group, the individual social phenotype, may be more important for fitness than the emergent group social phenotype.

**Key words:** fitness consequences, long-term study, social mammal, social network analysis, social structure, yellow-bellied marmot.

## INTRODUCTION

Dynamic social structures and relationships arise as a result of behavioral interactions between individuals (Hinde 1976), and social behavior and aggregation have demographic and evolutionary consequences (Alexander 1974; Wilson 1975; West-Eberhard 1979; Wey et al. 2008; Farine and Sheldon 2015). To advance our knowledge of the adaptive value of sociality, we must expand our understanding of precisely how animals are affected by their social interactions (Hinde 1976; Krause et al. 2007; Silk 2007; Croft et al. 2008; Kurvers et al. 2014).

Over the past decade social networks have been used to quantify a variety of measures of sociality and have shed novel insights on the adaptive value of sociality (Wey et al. 2008; Whitehead 2008; Pinter-Wollman et al. 2014; Croft et al. 2016). Prior work exploring the fitness consequences of sociality using animal social networks can be broadly summarized into three main areas: (1) how an individual's social interactions affect them (e.g., copulation

success in male forked fungus beetles (*Bolitotherus cornutus*; Formica et al. 2012), (2) how an individual's social mate's interactions affect them (e.g., survival in bottlenose dolphins (*Tursiops sp.*; Stanton and Mann 2012), and (3) how individual social interactions influence group and population processes (territory selection in great tits (*Parus major*); Farine and Sheldon 2015). In summary, the pattern and makeup of interactions individuals participate in has direct consequences on their fitness, the structure of their group, and population processes (Lusseau 2003; Oh and Badyaev 2010; Formica et al. 2012; Kurvers et al. 2014; Croft et al. 2016; Leu et al. 2016).

However, these prior network studies have largely overlooked the role of the social group as a whole in influencing an individual's success (i.e., group-level selection; Wilson 1983; Okasha 2006). That is, current animal behavior network research has under addressed how the resulting feedback from all the interactions between individuals in a group subsequently influences each individual who comprises the group. This is separate from asking how individuals contribute to the social structure—specific attributes of the pattern of all social interactions in a group—but

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instead explores the consequences of social structure, which is an emergent property (Moore et al. 1997; Kappeler 2019). Social structure, or the group's social phenotype, is more complex than averages of individual-level network values (the individual social phenotype). Therefore, to better map the consequences of sociality for individuals, the influence of social structure must be explored directly.

Prior research has already suggested a relationship between the social group and individual fitness correlates. For example, individuals residing in groups with regular intragroup conflict experience reduced reproductive opportunity and success and increased chronic stress in a variety of primates (de Waal 2000; Flack et al. 2006), as well as water striders (*Aquarius remigis*; Sih and Watters 2005) and meerkats (*Suricata suricatta*; Young et al. 2006). Although suggesting the social group may influence an individual's success, these studies did not identify specific attributes of the social group. Work on humans has quantified social structure via social network analysis and explored team success in English Premier League soccer (Grund 2012) and professional e-sports (Mora-Cantallos and Sicilia 2019), the vitality of Western Chinese housing markets (Zhang et al. 2012), the inefficiency of the U.S. Congress (Neal 2020), and work in non-human primates has explored the social structure factors impacting primate group size (Balasubramaniam et al. 2017) and movement patterns (Dufour et al. 2011). How animal's group social structures respond to altered ecological conditions (Leu et al. 2016; Costello et al. 2022) and how social structure emerges based on the group's composition of individual personalities (Cook et al. 2022) has also been quantified with social network analysis. Though, the connection between specific attributes of social structure and its fitness consequences is greatly understudied, in both humans and non-humans.

Reproductive success is a key fitness component (Clutton-Brock 1988). Different aspects of reproductive success are influenced by biotic and abiotic factors such as weather (Thompson 1997; Krüger 2002), prey and predator abundance (Lack 1947; Martin 1987; Durant 2000), and population density (Kunin 1997; Luijten et al. 2000). Reproductive success is also influenced by the performance and outcome of social behaviors (Alexander 1974; Silk 2007). Prior work has used social networks to explore this relationship on the individual level in a range of taxa including, but not limited to, some insects (Formica et al. 2012), lizards (Godfrey et al. 2012), birds (McDonald 2007; Ryder et al. 2008; Oh and Badyaev 2010), fishes (Solomon-Lane et al. 2015), and mammals (Silk et al. 2009; Wey et al. 2013; Wyman et al. 2021). These prior studies focused almost entirely on individual level sociality, and not that of group social structure.

Few studies have explored the social structure-fitness relationship. One such study explored displacement networks in captive bluebanded gobies (*Lythrypnus dalli*), an obligatorily social species, and identified a negative relationship between individual reproductive success and aggressive reciprocity (rate at which aggressive behaviors were both initiated and received between social ties across the group; Solomon-Lane et al. 2015). This study demonstrated how social network analysis can be applied to both describe the attributes of a group's social structure and quantify its consequences at the individual level. However, how this important relationship transpires in wild populations, or in facultatively social species, is not known. Here we explore the social structure-reproductive success intersection in a long-studied population of free-living wild yellow-bellied marmots (*Marmota flaviventris*), a facultatively social rodent.

Yellow-bellied marmots are an ideal system in which to study the consequences of social group structure for several reasons. First, they are socially plastic which creates variation in social structure (Blumstein 2013). Second, social connections at the individual level have been related to reproductive success. Males (who fight with other males to control matriline and gain or maintain reproductive access) who participate in more agonistic behaviors experience reproductive benefits (Wey and Blumstein 2012). Adult female marmots (the central figures in social groups) who are more social in affiliative (e.g., greeting, allogrooming, play) networks experienced reproductive deterrents (Wey and Blumstein 2012), potentially due to the time and energy costs of social interactions. This finding corroborated previous work in this system that found social factors differentially influenced reproductive success across sexes (Armitage 1991). Third, prior work in this system showed that group social structure is associated with a key fitness trait—the rate at which marmots gain mass in the summer, which is highly correlated with over-winter survival because fat reserves are the primary metabolic energy source during hibernation (Philson et al. 2022). Specifically, marmots residing in less connected, more socially homogeneous, and more stable social groups tended to gain less body mass during the summer growing season than those residing in social, heterogeneous, and unstable groups. Together, these past studies strongly suggest sociality has significant implications for marmot reproductive success and that social structure has the potential to influence reproductive success. These results also provide the background knowledge to develop specific hypotheses. Lastly, the long-term dataset on this population, with a large number of replicate social group measurements, and associated fitness measures over two decades, enabled us to explore the social structure-fitness relationship beyond a few social groups in laboratory settings.

We developed a priori hypotheses for the relationship between five attributes of social structure (density, transitivity, reciprocity, positive degree assortativity, and cut points; Table 1) and two measures of reproductive success in adult female marmots: (1) if offspring were successfully weaned and (2) the number of offspring weaned, if offspring were weaned. These five network measures have homologous measures on the individual level, which facilitated the development of a priori hypotheses as well as our understanding of the consequences of social behavior across social scales.

Our specific a priori hypothesis was that individuals in more connected and sociable groups would experience lower reproductive success. This hypothesis was informed by previous network studies in this system showing strong individual social relationships are often costly for reproductive success (Wey and Blumstein 2012) and that residing in connected groups reduced mass gain during the summer—a key fitness-related trait for marmots (Philson et al. 2022).

Also based on our previous social structure study (Philson et al. 2022), we hypothesized individuals residing in socially homogeneous groups would experience higher reproductive success. Social homophily within a group may lead to a reduction in social stressors because interactions are more predictable and reliable (Massen and Koski 2014). Additionally, less stressed female marmots have higher reproductive success (Monclús et al. 2011; Blumstein et al. 2016; Pinho et al. 2019). Being surrounded by similarly social individuals may facilitate avoidance of stressful and aggressive interactions and instead allow for more time and energy to be allocated towards tending to offspring. Thus, we hypothesized social homophily would enhance reproductive success.

**Table 1**

**Network-level measures used to quantify social structure along with the a priori hypothesized direction of the relationship between the social measure and reproductive success**

| Measure              | Description   | References  | Interpretation   | Hypothesized Direction |
|----------------------|---|---|--|------------------------|
| Density              | Number of interactions observed represented as a fraction of all possible interactions  | Burt 1992; Wasserman and Faust 1994; Grund 2012                           | How connected a group is   | –                      |
| Transitivity         | Proportion of completely connected triads out of the total possible triads              | Wasserman and Faust 1994; Milo et al. 2002; Faust 2010                    | How cyclically connected a group is. There are more transitive components in affiliative networks in this system (Wey et al. 2019) | –                      |
| Reciprocity          | The number of mutual interactions divided by the number of possible mutual interactions | Wasserman and Faust 1994; Solomon-Lane et al. 2015; Squartini et al. 2013 | Used to quantify how mutual or one-sided interactions are in a group   | +                      |
| Degree Assortativity | Tendency for social ties to share similar individual degree measures                    | McPherson et al. 2001; Currarini et al. 2016                              | How socially homogeneous a group is, in terms of individual’s number of social partners  | +                      |
| Cut points           | Number of social ties that if cut will result in two or more separate networks.         | Wasserman and Faust 1994; Borgatti 2006                                   | How stable or fragmentable (breakable) a group is  | +                      |

Finally, we hypothesized that attributes of social structure would be more strongly related to the number of offspring that weaned from the burrow than it would be related to whether an individual successfully weaned offspring. Individuals that are involved in many interactions may become socially stressed, energetically depleted, and may have less time and energy for parental care, and consequently may wean fewer offspring. Thus, variance in the number of offspring weaned may be explained more by attributes of social structure than if an individual weaned any offspring at all.

Overall, this work will help us contextualize the potential role that social structure, an emergent property, plays in influencing reproductive success. By doing so, it adds to our understanding of the adaptive value of sociality across social scales. We use a well-studied population of a wild social mammal with a large number of replicate social groups across 20 years to address this question.

**METHODS**

**Data collection**

The yellow-bellied marmot population around the Rocky Mountain Biological Laboratory (RMBL) in the Upper East River Valley, Gothic, Colorado (38°57’N, 106°59’W; ca. 2900 m elevation) has been continuously studied since 1962. Yellow-bellied marmots are a facultatively social, harem-polygynous species of ground-dwelling squirrel that live in matrilineal colonies with one or two territorial males (Frase and Hoffmann 1980; Armitage 1991). Active for five months annually (early May to mid-September), marmots mate soon after emerging from hibernation, with new pup emergence and yearling dispersal occurring around late-June/early-July. Annually, nearly half of females and most males disperse with most dispersal resulting in movement out of the study area (Armitage 1991).

From 2002 to 2020, marmots were observed and repeatedly live trapped during their active season. Using Tomahawk-live traps placed near burrow entrances, individuals were trapped and immediately transferred to cloth handling bags to record body mass, sex, and other morphological and physiological measures. Only adults are reproductively mature (pups < 1 year, yearlings = 1 year, and adults ≥ 2 years. All marmots are given two uniquely numbered permanent metal ear tags (Monel self-piercing fish tags #3, National Band and Tag, Newport, KY) and marked on their dorsal pelage

with nontoxic Nyanzol fur dye (Greenville Colorants, Jersey City, NJ) to aid identification from a distance. Virtually all marmots in our study population are trapped and marked annually, permitting us to accurately identify interacting individuals. Because most other marmots at each colony site were marked, we can often identify the individuals that may have not been recaptured after molting their pelage (and thus marks). Colony sites can be grouped into a higher classification of higher elevation and lower elevation sites (five are at higher elevation sites, seven are at lower elevation sites). Higher elevation sites are ~166 m higher than lower elevation sites and experience harsher weather conditions (Van Vuren and Armitage 1991; Blumstein et al. 2006; Maldonado-Chaparro et al. 2015b).

Detailed social interactions in this population have been recorded since 2002. Behavioral observations are made during hours of peak activity (07:00–10:00 h and 16:00–19:00 h; Armitage 1962) using binoculars and spotting scopes from distances that did not disrupt normal social behavior (20–150 m; Blumstein et al. 2009). We classified each interaction as either affiliative (e.g., greeting, allogrooming, play) or agonistic (e.g., fighting, chasing, biting; detailed ethogram in Blumstein et al. 2009). We also recorded the initiator and recipient, time, and location of each interaction. Most interactions (79%) occurred between identified individuals. The direction of the remaining 21% interactions could not be identified because the marmot’s dorsal fur mark was not visible, due to the marmot’s posture or visual obstructions, and thus we excluded these interactions from our data. Excluding these interactions between unidentified individuals should not significantly influence social structure (Silk et al. 2015). Our data also only consisted of yearlings and adults because these cohorts were present early in the season, when social interactions were the most common. We excluded pups from our data because of their mid-season emergence and as they primarily only interact with each other and their mother (Nowicki and Armitage 1979). Additionally, we filtered out individuals observed or trapped fewer than five times in a year to eliminate those dispersing through the study area (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018).

**Social network measures**

Using this refined social observation data collected from 2002 to 2020 and the R package “igraph” (Csardi and Nepusz 2006; version

1.2.11; R Development Core Team 2021; version 4.1.2), weighted (accounting for the number of interactions in a social connection) and directed (accounting for who initiates and receives each interaction) social interaction matrices were constructed from affiliative interactions between individuals for each year. We focused on affiliative interactions because they relate to female marmot reproductive success on the individual level (Wey and Blumstein 2012) and because they comprised 88% of interactions in our refined data. These affiliative matrices consisted of 38 968 social interactions between 726 individuals (626 of whom were observed across multiple years). 18 438 of these interactions and 313 unique individuals were at our lower elevation sites and 20 530 interactions and 417 unique individuals were at the higher elevation sites. From these matrices, we defined a social group as each network isolate (set of connected individuals with no other external connections) that appeared naturally within a valley location (higher elevation or lower elevation; Philson et al. 2022) in a given year. This produced 137 social groups in total. The number of social groups that emerged from a valley location ranged from 1 to 6, whereas the total number of social groups in our study area annually ranged from 4 to 11. Group sizes ranged from 3 to 58 individuals with a mean of 20.51 (SE = 0.52) across the dataset.

For each social group we calculated five social network measures to quantify social structure (described in Table 1). Density, transitivity, and cut points represent specific attributes of connectivity; reciprocity and degree assortativity represent specific attributes of homophily. We selected these five social network measures due to their importance in past papers in our system (transitivity: Wey et al. 2019; density, transitivity, cut points, reciprocity, and degree assortativity: Philson et al. 2022), other systems (density: Weinig et al. 2007; reciprocity; Soloman-Lane et al. 2015) and/or because these network measures have analogous measures on the individual level, aiding our understanding of consequences of social behavior across social scales (Wasserman and Faust 1994). Our observations of marmot social groups across their entire active season (mean  $n$  observations per individual across years = 28.81, range of each year = 6.79–75.14) and low rate of unknown individuals involved in social interactions facilitated the reliability of the five social network measures (Silk et al. 2015; Davis et al. 2018; Sánchez-Tójar et al. 2018). Because some network measures cannot be calculated for certain group sizes or group configurations (e.g., transitivity for a group of two or a linear group) we systematically removed all N/A's for network measures from the data. If an individual had an N/A in any of its measures, it was removed from the data entirely. This can be attributed to some individuals only being observed a few times a year or their membership in a small group (e.g., a group of two; Wasserman and Faust 1994).

Because group size is associated with many social network measures (Wasserman and Faust 1994; e.g., density, cut points), as seen in previous analyses in our system (Maldonado-Chaparro et al. 2015a), we ensured each measure was standardized for group size by dividing the social network measures by group size. Some measures already are “standardized” because of how they are calculated (density, reciprocity, and transitivity; Wasserman and Faust 1994). Thus, we manually divided degree assortativity and cut points by group size so all five of our network measures were standardized for group size.

## Reproductive success

Although both males and females are in the social networks, we focus only on female reproductive success because male reproductive success mostly depends on dominance and tenure length

(Armitage 1998; Huang et al. 2011). Yellow-bellied marmots are harem-polygynous; males fight for control of harems with more aggressive males with better body conditions experiencing greater reproductive success (Huang et al. 2011). Additionally, the smaller number of males in the population diminishes analysis power, requiring models with different covariates from the female models and thus inhibiting comparisons between sexes. We focused on two attributes of female reproductive success: (1) a binary measure if a female successfully weaned a litter from the burrow and (2) if a female successfully weaned a litter, a continuous measure of the number of pup/s that weaned. Offspring were assigned to each female based on behavioral observations and a comprehensive pedigree (see Blumstein et al. 2010 and Olson and Blumstein 2010 for pedigree details). Because we use weaned pups for both measures, this methodology does not account for pups that may have been born in the burrow but died before emergence (i.e., weaned; all pups are born in the burrow and emerge ~30 days after birth; Armitage 2014).

## Data analysis

To test the relationships between social structure and female reproductive success, we fitted two (one for each measure of reproductive success) generalized linear mixed models in R using the “lme4” package (Bates et al. 2015b; version 1.1-27.1). Whether a female successfully weaned offspring from the burrow was the first dependent variable. We fitted a binomial distribution using the “logit” link function and a bobyqa optimizer with 1000 function evaluations (Bates et al. 2014, 2015a). This model had 654 observations of female reproductive success and group measures consisting of 306 unique individuals in 92 social groups across 19 years. For the females that had pup/s wean from the burrow, our second dependent variable was the number of pup/s that weaned. We fitted a Poisson distribution using the “log” link function. This model had 234 total observations of female reproductive success and group measures consisting of 109 unique individuals in 78 social groups across 19 years.

Both models included the five network measures, group size (number of individuals in the social group), age, June mass, and valley location as fixed effects. We included the individual attributes June mass, age, and location because the correlates of reproductive success are multicausal and we want to account for these important attributes. Group size was included as a fixed effect due to its relationship with fitness correlates in this system (Wey and Blumstein 2012; Maldonado-Chaparro et al. 2015a). Age was included because older females are more likely to wean smaller litters than younger mothers under stressful conditions (Monclús et al. 2011) and because marmots become less social as they age (Wey and Blumstein 2010). Age was squared in our models to account for senescent declines as female reproductive success increases linearly with age until age seven, at which point female reproductive success declined (St. Lawrence et al. 2022). June mass was included because adult relative mass is positively associated with annual reproductive success (Huang et al. 2011; Blumstein et al. 2016).

We included year and individual ID as random effects (random effects were crossed as an individual may be seen in multiple years). We included year as a random effect to acknowledge annual environmental and demographic differences (Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger et al. 2020). Individual identity was included as a random effect to account for individuals that were observed over multiple years. Although using social group ID would have accounted for multiple members of the



**Table 2**

Model estimates, standard error, *P* value, marginal and conditional part *R*<sup>2</sup> values for both models. Values in bold represent statistical significance (*P* < 0.05). In addition to estimated part *R*<sup>2</sup> and semi-partial part *R*<sup>2</sup> values, estimated 95% confidence intervals based on 100 parametric bootstrap iterations are reported in parentheses. The model exploring if offspring were successfully weaned had 654 observations of female reproductive success and group measures consisting of 306 unique individuals in 92 social groups across 19 years. The model exploring the number of offspring weaned had 234 total observations of female reproductive success and group measures consisting of 109 unique individuals in 78 social groups across 19 years

|               | If offspring were successfully weaned           |                  |                             |                                | Number of offspring weaned                      |                  |                             |                                |
|---------------|---|------------------|-----------------------------|--------------------------------|---|------------------|-----------------------------|--------------------------------|
|               | 654 observations of female reproductive success |                  |                             |                                | 234 observations of female reproductive success |                  |                             |                                |
|               | Est. ± SE                                       | <i>P</i> Value   | Marginal PartR <sup>2</sup> | Conditional PartR <sup>2</sup> | Est. ± SE                                       | <i>P</i> Value   | Marginal PartR <sup>2</sup> | Conditional PartR <sup>2</sup> |
| Intercept     | -1.328 ± 0.22                                   | <b>&lt;0.001</b> | 54.48% (47.76%–65.09%)      | 61.71% (51.23%–70.51%)         | 1.572 ± 0.047                                   | <b>&lt;0.001</b> | 13.78% (9.96%–24.39%)       | 23.5% (14.63%–36.7%)           |
| Density       | -0.345 ± 0.408                                  | 0.398            | 0% (0%–28.39%)              | 7.21% (0%–29.63%)              | -0.087 ± 0.109                                  | 0.422            | 0.44% (0%–12.5%)            | 10.17% (0%–25.4%)              |
| Transitivity  | 0.173 ± 0.244                                   | 0.478            | 0% (0%–28.2%)               | 6.94% (0%–29.43%)              | 0.082 ± 0.065                                   | 0.208            | 0.77% (0%–12.77%)           | 10.49% (0.02%–25.68%)          |
| Reciprocity   | 0.061 ± 0.189                                   | 0.746            | 0% (0%–28.39%)              | 7.22% (0%–29.64%)              | 0.051 ± 0.045                                   | 0.252            | 0.55% (0%–12.58%)           | 10.27% (0%–25.49%)             |
| Cut Points    | -0.172 ± 0.181                                  | 0.343            | 0.59% (0%–28.79%)           | 7.82% (0%–30.08%)              | 0.091 ± 0.044                                   | <b>0.037</b>     | 1.51% (0%–13.39%)           | 11.24% (0.76%–26.3%)           |
| Degree        | 0.178 ± 0.187                                   | 0.341            | 0.31% (0%–28.61%)           | 7.54% (0%–29.88%)              | -0.02 ± 0.043                                   | 0.636            | 0.13% (0%–12.24%)           | 9.83% (0%–25.13%)              |
| Assortativity |   |                  |                             |                                |   |                  |                             |                                |
| Group Size    | -0.556 ± 0.293                                  | 0.058            | 0.67% (0%–28.85%)           | 7.9% (0%–30.15%)               | -0.072 ± 0.078                                  | 0.361            | 0.65% (0%–12.67%)           | 10.37% (0%–25.57%)             |
| Valley        | -0.019 ± 0.162                                  | 0.909            | 0.1% (0%–28.46%)            | 7.33% (0%–29.72%)              | 0 ± 0.04  | 0.998            | 0% (0%–12.13%)              | 9.72% (0%–25.02%)              |
| Location      |   |                  |                             |                                |   |                  |                             |                                |
| June Mass     | 1.755 ± 0.341                                   | <b>&lt;0.001</b> | 15.92% (0%–39.12%)          | 23.15% (3.91%–41.59%)          | 0.177 ± 0.045                                   | <b>&lt;0.001</b> | 4.87% (0.16%–16.29%)        | 14.59% (4.56%–29.15%)          |
| Age           | 0.786 ± 0.259                                   | <b>0.002</b>     | 0% (0%–26.22%)              | 4% (0%–27.22%)                 | -0.064 ± 0.045                                  | 0.148            | 0% (0%–11.92%)              | 9.47% (0%–24.81%)              |

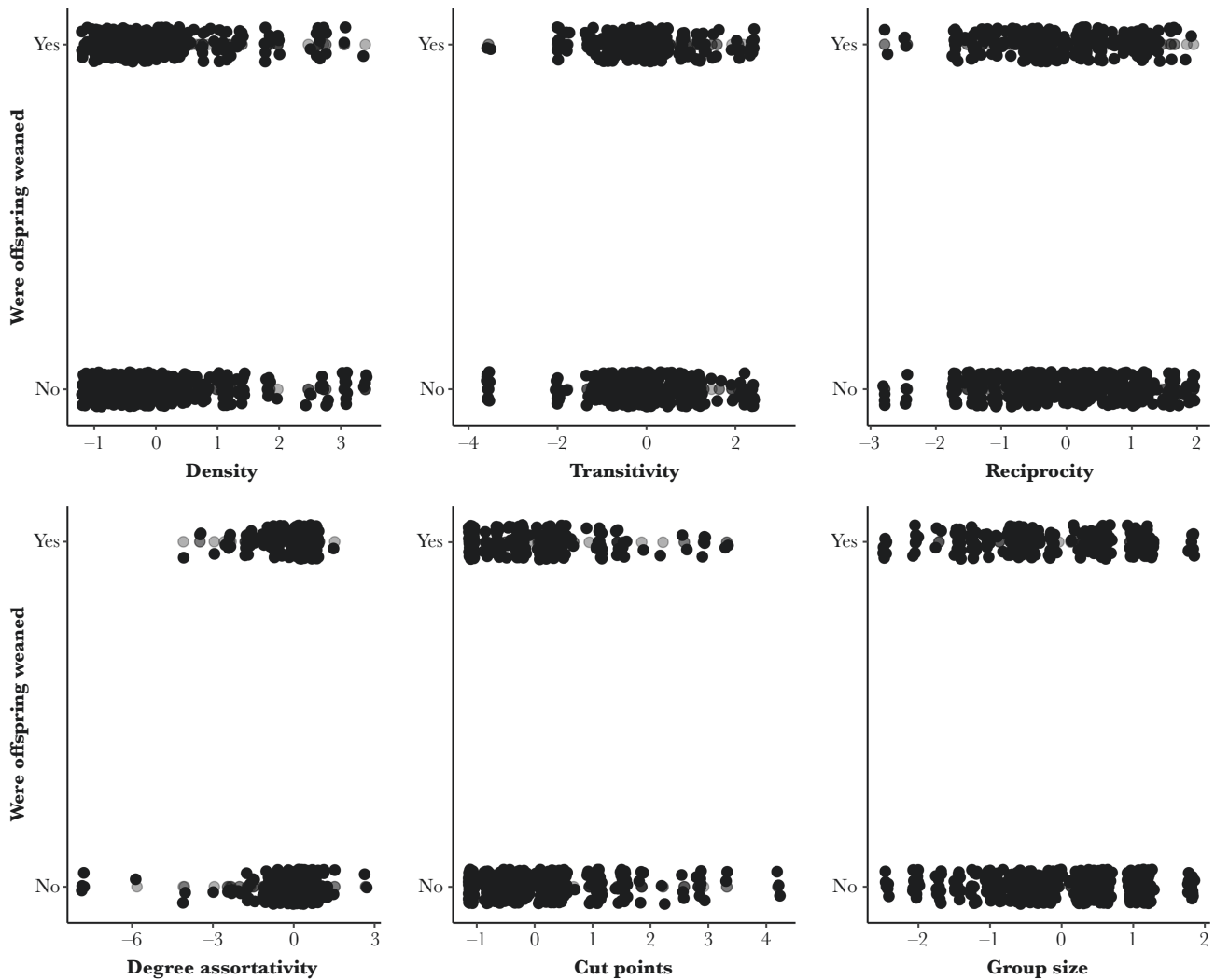
same group that shared a network measure within a given year (as done in Philson et al. 2022), we did not include this as a random effect due to model convergence and overfitting issues. When we do fit our two models with social group ID, despite model fitting issues, results of our models did not change and <0.93% of additional conditional variance was explained in both models. Because of this, and because we control for individuals within and across years, we are confident that by not including social group ID we are not misrepresenting our results or attributing all among-group differences to the network traits. Additionally, groups often have one or few reproductive females, thus there is little to no variation of within group reproductive success that requires explanation, further bolstering our confidence that the exclusion of group ID is not creating misleading results.

Valley location was our only categorical fixed effect and we mean-centered it after Schielzeth (2010); lower elevation sites were coded as “+1” whereas higher elevation sites were coded as “-1”. Group size and age were log<sub>10</sub> transformed and all variables then were standardized (mean-centered and divided by one SD using the “scale” function in base R; Becker et al. 1988). We checked for collinearity by calculating correlation coefficients between continuous predictors. We originally attempted to fit models with two additional network measures (average path length and centralization), though due to their high correlation coefficient of >0.8 with other network measures (group size and degree assortativity, respectively), we did not include average path length and centralization in our models (Franke 2010; Shrestha 2020). After fitting each model, we checked model assumptions with the “check\_model” function in the “performance” package in R (Lüdtke et al. 2021). We calculated the marginal and conditional *R*<sup>2</sup> values for the whole model and calculated the semi-partial marginal and conditional *R*<sup>2</sup> to estimate the variance explained by each of our fixed effects using the “partR2” package in R (Nakagawa and Schielzeth 2013; Stoffel et al. 2021; version 0.9.1). The marginal *R*<sup>2</sup> gives an estimate of the variance explained by all fixed effects for the model. The conditional *R*<sup>2</sup> gives an estimate of the variance explained by all fixed effects plus all random effects for the model. The marginal semi-partial *R*<sup>2</sup> gives an estimate of the variance explained by each individual fixed effect whereas the conditional semi-partial *R*<sup>2</sup> gives an estimate of the variance explained by each individual fixed effect plus the variance explained by all the random effects. We use marginal semi-partial *R*<sup>2</sup> values in the remainder of the primary text, and report conditional semi-partial *R*<sup>2</sup> values in Table 2. We estimated 95% confidence intervals for our *R*<sup>2</sup> and semi-partial *R*<sup>2</sup> values using 100 parametric bootstrap iterations. The figures were generated using “ggplot2” package in R (Wickham 2016; version 3.3.5).

## RESULTS

### Social structure is not associated with the number of offspring weaned

We found no significant main effects of social structure in our model for whether a female successfully weaned offspring (Figure 1; Table 2), suggesting social structure does not play a primary role in successfully weaning a litter. Our model explained 54.48% of the marginal variance and 61.71% of the conditional variance. These results thus reject our a priori hypotheses which stated that female marmots in more connected and less homogeneous groups would have reduced reproductive success.



**Figure 1**

Relationship between whether offspring were weaned and social structure. The predictor variable is scaled (mean-centered and divided by one SD); the response variable is binary (1 = weaned a litter, 0 = did not wean a litter). Darker points indicate more overlaid data whereas lighter points indicate less overlaid data.

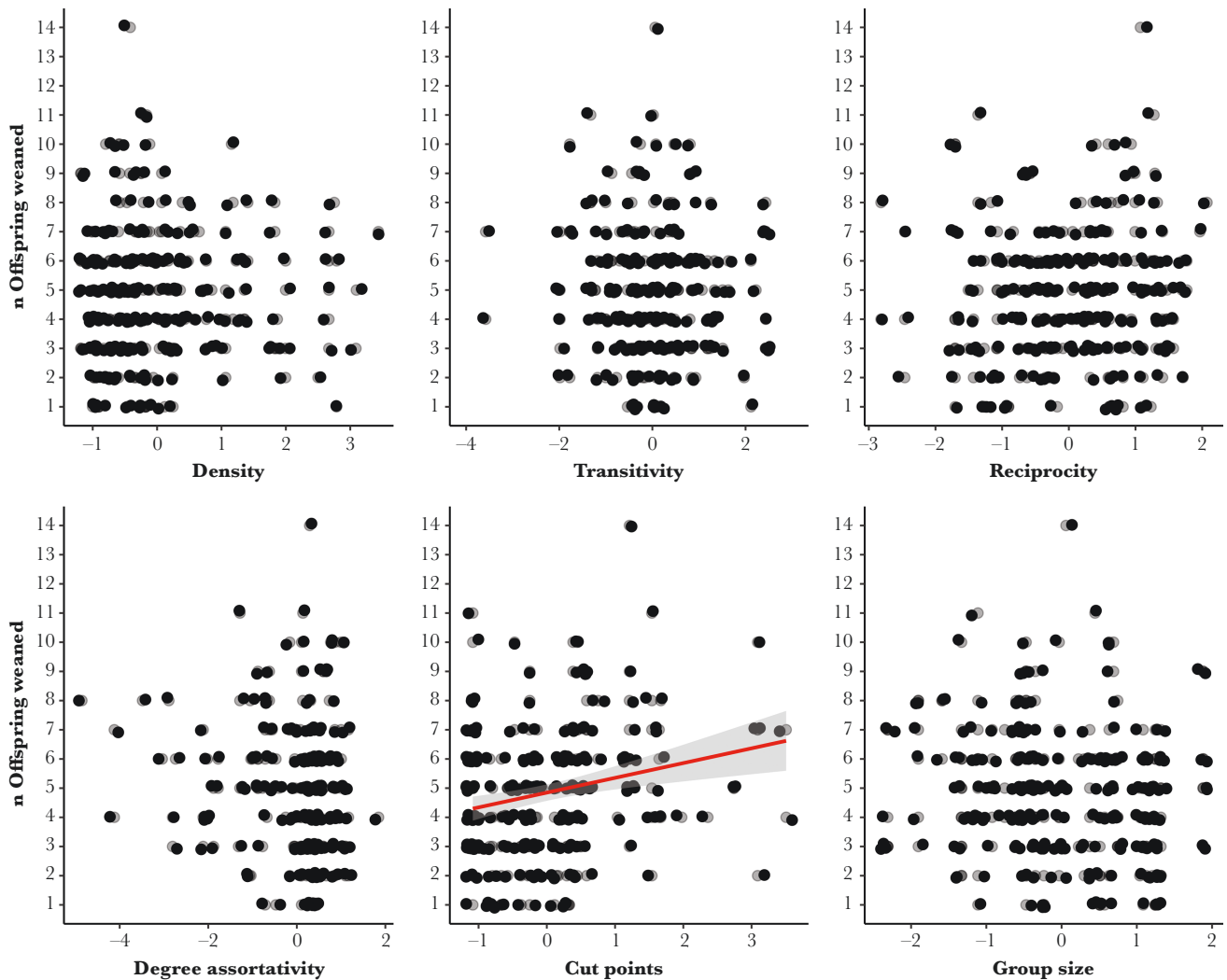
### Breakable social structures are modestly associated with the number of offspring weaned

Overall, four of the five measures of social structure did not have a significant statistical relationship with the number of offspring weaned. However, one did; there was a statistically significant positive main effect of cut points on the number of offspring weaned ( $B = 0.091$ ;  $P = 0.037$ ; Std. Error = 0.044; Figure 2; Table 2). This suggests as social groups become more fragmentable (i.e., breakable into two or more separate groups of two or more individuals), females may have higher reproductive success. This result is consistent with our a priori hypothesis. This model had a marginal  $R^2$  value of 13.78% and a conditional  $R^2$  value of 23.50%. Cut points as a fixed effect alone explained 1.51% of the marginal semi-partial  $R^2$  variance suggesting that the effect is relatively modest.

## DISCUSSION

In exploring the relationship between group social structure and reproductive success in a facultatively social rodent, only one measure

of social structure was related with female reproductive success suggesting that, overall, group structure has a limited impact on this key fitness attribute in yellow-bellied marmots. Social structure is an emergent property of the group and thus exists on a different phenotypic scale than an individual's direct social interactions (Moore et al. 1997; Croft et al. 2016; Kappeler 2019). In this system, how many social partners an individual has, how often they interact with their social partners, and their position within their group are much stronger predictors of reproductive success (Wey and Blumstein 2012), and fitness overall (alarm call propensity: Fuong et al. 2015; survival: Yang et al. 2017; longevity: Blumstein et al. 2018), than social structure. Individual social phenotypes (e.g., individual position) playing a more consequential role than group social phenotypes (e.g., social structure) is not unexpected (Wilson 1983; Okasha 2006). Although residing in a certain type of group may have some effect, in species with low intergroup interactions, such as our system, an individual's direct social interactions are more impactful on an individual's fitness than an emergent property like social structure. Our results imply that, although potentially important, group-level selection is less evolutionarily consequential than



**Figure 2** Relationship between the number of offspring weaned and social structure. The predictor variable is scaled (mean-centered and divided by one SD); the response variable is a count. A predicted regression (with 95% CIs) is plotted for the significant relationship and was created using R package “sjPlot” (Lüdtke 2022) to account for both fixed and random effect. Darker points indicate more overlaid data whereas lighter points indicate less overlaid data.

individual-level selection in the context of reproductive success, at least in this facultatively social mammal. This is not to say that this group-level selection plays no role because growing evidence shows that both individual and group traits both influence individual fitness (Lusseau 2003; Oh and Badyaev 2010; Formica et al. 2012; Kurvers et al. 2014; Solomon-Lane et al. 2015; Croft et al. 2016; Leu et al. 2016; Philson et al. 2022), often differentially (Goodnight et al. 1992; Weinig et al. 2007; Laiolo and Obeso 2012). Thus, more research in this system and others should incorporate measures of both individual position and group social structure to better understand the directional selection on these two scales of social phenotypes.

Our modest statistically significant positive relationship between female reproductive success and group social structure (Figure 2; Table 2) suggests that females in groups with more cut points wean larger litters. Thus, as social groups become more fragmentable (breakable into two or more separate groups), females may experience higher reproductive success. This result supports our specific a priori hypothesis for cut points, though with the other network

measures having no significant statistical relationship with reproductive success, we mostly reject our broader a priori hypothesis that social structure is generally related to female reproductive success. Our two measures of reproductive success happen after social behavior seasonally attenuates in this system. It is possible that reproductive events more closely tied to peak social activity (e.g., the likelihood of mating) could result in stronger associations.

The cut points result is interesting for a few reasons. Females in more fragmentable groups experiencing a fitness benefit align with our previous study of the social structure-fitness relationship in this system which showed that marmots have higher rates of proportional mass gain in more fragmentable and less social groups (Philson et al. 2022). These two sets of results are plausible because yellow-bellied marmots are facultatively social and experience many fitness costs from being more connected on the individual level (decreased female reproductive success: Wey and Blumstein 2012; decreased winter survival: Yang et al. 2017; shorter lifespan: Blumstein et al. 2018). Because marmots may mostly gain anti-predator benefits from social living, and because

alarm calls can be heard across separate social groups (Armitage 2014), residing in fragmentable groups may limit the costs of increased sociality. This study and our previous study show marmots may experience fitness costs from residing in more connected groups as well, adding to our understanding of the adaptive value of sociality across social scales (Blumstein 2013). The tools and implications of our work extend to more social species, especially in species for which work has focused on implications of social interactions on the individual level. Thus, to comprehensively understand the consequences of sociality, group social structure must be explored in both facultatively and obligatory species in the wild.

Reproductive suppression may also play a role in our results. Reproductive suppression is widely reported in social animals, including rodents (Solomon and French 1997; Hacklander et al. 2003). When closely living females compete reproductively, not all females may breed or litter sizes are reduced (Hacklander et al. 2003). Despite affiliative interactions being more likely between related females due to the matrilineal nature of yellow-bellied marmot social groups (Armitage 1998), older females have been shown to suppress their daughters' reproduction (Armitage 1991). The statistical significance of age in our model exploring if a female reproduced may be partly related to this age-based suppression. Additionally, the positive statistical significance of body mass in both models suggests larger females experience higher reproductive success, and when thinking about reproductive suppression, may be better able to suppress smaller females. The main effect of cut points—females residing in more fragmentable groups wean larger litters—also fits in with the reproductive suppression seen in this system. Residing in more fragmentable groups may limit the social opportunities for older females to suppress younger females' litter sizes. The social environment is primary predictor of female-female reproductive suppression in some primates (Beehner and Lu 2013), carnivores (Montgomery et al. 2018), and rodents (Sherman 1981; Wolff 1993; Wolf 1997; Freeman 2021). More fragmentable groups may be spread across a larger area, potentially leading to younger females raising litters in burrows separate from their mothers, facilitating reproductive suppression avoidance. As female marmots age, they become less social (Wey and Blumstein 2010), and this may further provide less social opportunity for older females to reproductively suppress younger females, which may be compounded in fragmentable groups. For younger females, fewer interaction opportunities with older females may also allow for unrestricted mating with the dominate male (often their father, whom they will mate with), or, in groups that contain multiple males, with sub-dominant males.

In summary, we found that group social structure is only modestly associated with higher reproductive success. Nevertheless, this work is a valuable addition to analysis of the fitness consequences of the individual social phenotype and has larger evolutionary implications, namely it has increased our understanding of the consequences of social behavior across social scales. This work is also consistent with the observation that although potentially important, group-level selection is often less evolutionarily consequential than individual-level selection (Okasha 2006). However, this does not mean emergent properties like social structure should not be explored (Kappeler 2019). Because both individual and group traits influence individual fitness, often differentially, more basic research across animal systems is required to better understand social structure's relationship with fitness. Ultimately, this understanding

will enhance our understanding about the selection on individual and group social phenotypes across animal systems.

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

Data availability: Analyses reported in this article can be reproduced using the data provided by Philson and Blumstein (2022).

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