Animal Behaviour 201 (2023) 63–72

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The (surprising) importance of males in a matrilineal society: behavioural insights from a topological knockout study

Friederike Zenth [a, 1], Adriana A. Maldonado-Chaparro [b, c, 1], Ana Solis [c], Stephanie Gee [c], Daniel T. Blumstein [c, d, *]

[a] Department of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany
[b] Department of Biology, Faculty of Natural Sciences, Universidad del Rosario, Bogota D.C., Colombia
[c] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.
[d] Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.

ARTICLE INFO

Article history:
Received 4 July 2022
Initial acceptance 9 September 2022
Final acceptance 21 March 2023

MS. number: A22-00333R

Keywords:
demographic social role
social dynamics
social structure
statistical knockout experiment

Social group structure often has consequences for individual fitness and ecological and evolutionary processes, but group structure is not fixed because of demographic processes: individuals die, disperse or are recruited into social groups. Thus, it is important to understand how demographic social roles and the loss of individuals with different roles modify group structure. We studied yellow-bellied marmots, *Marmota flaviventer*, and performed a series of statistical/topological knockouts on observed marmot social networks to investigate how the social roles of individuals from specific age–sex categories (adult/yearling, males/females) contribute to group social structure and to ask whether the loss of different roles has varying structural effects. We focused on five central aspects of overall social structure: density, the global clustering coefficient, reciprocity, global degree centrality and the coefficient of variation of strength. Somewhat surprisingly, given that marmots live in matrilines, our knockout results suggested that males played a key role in shaping networks: yearling males were a key cohesive element and adult males were central players in agonistic networks. Thus, social networks are dynamic and their structure is shaped in the interplay of demographic processes and individual social behaviour.

Conspecific social relationships are a central component of the ecology of social animals. Individuals of a species may cooperate to exploit resources, withstand harsh environments or avoid predation; they also compete with each other for resources and reproductive opportunities. Thus, social structure, that is, the quantity, quality and patterning of social relationships (Hinde, 1976), directly and indirectly affects individual fitness (Gerber et al., 2022; Lehmann et al., 2016; Silk et al., 2009, 2010; Wey & Blumstein, 2012) and broader ecological and evolutionary processes (reviewed in Kurvers et al., 2014). Yet, questions remain about the processes that govern its formation, stability and dynamics.

Social structure emerges from individual social interactions and behavioural strategies (Bradbury & Vehrencamp, 2014; Lusseau, 2003), where the latter are often related to intrinsic characteristics, such as age, sex, body size, reproductive status or kinship (see Sosa (2016), for other characteristics). For example, males and females follow different reproductive behavioural strategies (Cords, 2002; Gouzoules et al., 1982), and relationships and behavioural strategies may change with age (Murphy et al., 2020; Wey & Blumstein, 2010). Thus, individuals may have different functions related to their position in the group; that is, adopt different social roles depending on age or sex, and these roles may vary in their importance to group social structure (Lusseau & Newman, 2004). In this context, previous studies have mostly focused on 'keystone' individuals who disproportionately affect other group members and group dynamics relative to their abundance, as well as levels of organization within the social system (Modlmeier et al., 2014). For example, in African elephants, *Loxodonta africana*, the oldest female acts as the keystone individual, and groups with older matriarchs have higher fitness than those without, probably because the oldest individual in a group of social mammals can affect the social knowledge of the group as a whole (McComb et al., 2001). However, there is a growing appreciation that not just key players, but more generally, demographic roles (different age–sex cohorts) shape

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* Corresponding author.
E-mail address: marmots@ucla.edu (D. T. Blumstein).

[1] Co-first authors.

https://doi.org/10.1016/j.anbehav.2023.04.013

animal social structure (Borgeaud et al., 2017; reviewed in Shizuka & Johnson, 2020).

Understanding how different age–sex cohorts contribute to shaping social structure is particularly relevant to understand how social structure responds to demographic processes (individuals are born, die or move between groups) that are inherent to any population. Moreover, besides naturally occurring demographic variation, group membership is increasingly impacted by human activities (Maldonado-Chaparro et al., 2021). For example, hunting and poaching pose additional sources of mortality for many wildlife populations that often selectively target specific age–sex classes related to desirable features such as big size or trophies (Coltman et al., 2003; Milner et al., 2007). On a larger scale, anthropogenically mediated natural disasters or disease epidemics increasingly impact wildlife populations by causing above-average mortality rates (Butler, 2018; Milligan et al., 2009; Testard et al., 2021), and, in some cases, demographic shifts if individual vulnerability is related to age and/or sex (e.g. Gould et al., 1999). Such changes directly affect social structure, through the gain or loss of group members and their social connections, where overall impacts are expected to vary depending on the direction of demographic shifts, in combination with species-specific demographic roles.

Social network analysis allows us to evaluate precisely how different individuals or social roles maintain group cohesion (Lusseau & Newman, 2004). Furthermore, social network analysis can capitalize on natural (e.g. death, dispersal), targeted or statistical/topological (i.e. simulated) removals of specific individuals to explore the varying effects that individuals have on a social network. These approaches are complementary. Topological knockouts elucidate direct effects of removing an individual and its social connections from a network. Thus, they also provide information about the structural contribution to and systemic role of a knocked-out individual in their network (Flack et al., 2006; Lusseau, 2003). In contrast, natural knockout experiments often do not control for direct effects of removing an individual from the group but reflect the outcome of their interplay with indirect effects of individuals responding to perturbations by readjusting their social behaviour with the remaining group members (Flack et al., 2006). From a practical viewpoint, topological knockouts are usually more feasible, particularly when working with wild populations (but see Firth et al., 2017).

Previous studies have capitalized on natural deaths, topological knockouts, experimental removals and illegal poaching to explore changes is social structure following the removal of specific individuals. For example, in orcas, *Ornicus orca*, topological removal of juveniles resulted in more fragmented social groups, illustrating that the number of social connections that whales have within their groups differs (Williams & Lusseau, 2006). In chacma baboons, *Papio ursinus*, surviving females became more 'cliquish' in their spatial associations after the death of a high-ranking female (Barrett et al., 2012). In captive pigtailed macaques, *Macaca nemestrina*, experimental and topological knockouts of individuals that participated in third-party policing resulted in less integrated societies and increased the likelihood of group destabilization, indicating that 'policers' help maintain a stable social network (Flack et al., 2006). In contrast, in African elephants, targeted poaching of older females, despite their key role in the society, did not impair hierarchical social structure, because daughters took over their mothers' positions (Goldenberg et al., 2016). This illustrates how the ability to behaviourally adjust and rewire existing social relationships in response to perturbations contributes to network resilience (Firth et al., 2017; Goldenberg et al., 2016; Testard et al., 2021). Thus, methodologically, while results of topological studies need to be interpreted carefully regarding real-life group responses to perturbations, reconfiguration effects may bias (natural) knockout experiments when inferring the importance of knockout nodes and the conditions under which such processes are possible.

Here we evaluate the direct effects of the loss of individuals of different age–sex categories (their demographic role) in shaping the social structure of yellow-bellied marmot, *Marmota flaviventer*, colonies. These large, ground-dwelling sciurid rodents are facultatively social, and prior work has shown that individuals of different age–sex categories behave differently and that group composition varies as a result of demographic events (Armitage, 2014). Yearlings are important in network cohesion and are the primary receivers of affiliative interactions, whereas adults decrease cohesion through agonistic and competitive interactions (Blumstein et al., 2009; Wey & Blumstein, 2010). Females may recruit daughters to their social group, thereby forming matrilines (Armitage & Schwartz, 2000), whereas most sons disperse as yearlings (Armitage, 1991). Thus, groups are not static over time.

We systematically removed social observations from specific individuals to investigate how these virtual removals (i.e. topological knockouts) affected different aspects of a group's social structure. We focused on the following network level measures: (1) density (a measure of the overall connectedness of a network), (2) the global clustering coefficient (network cohesion), (3) reciprocity (mutuality of relationships), (4) global degree centrality (the extent to which a network is dominated by the most 'popular' individuals) and (5) the coefficient of variation (CV) of individual strength (heterogeneity in sociality among individuals). Based on previously published correlative results (Wey & Blumstein, 2012), we hypothesized that individual yellow-bellied marmots of different age–sex categories contribute unevenly to the maintenance group structure and that such effects vary between affiliative and agonistic networks. Moreover, because yearlings are more socially active (Wey & Blumstein, 2010), we expected them to have a relatively large influence on the cohesiveness of affiliative networks, and because adult females maintain the social hierarchy (Armitage, 2014), we expected them to play an important role in structuring the group's agonistic networks. Finally, we predicted that because adult males defend one or more matrilines (female kin groups; Armitage, 2014), they would play a larger role in maintaining the structure of a group's affiliative network.

METHODS

Study System

We studied a free-living population of yellow-bellied marmots, located in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado, U.S.A. (38°57′29″N; 106°59′06″W), where they have been studied since 1962 (Armitage, 2014). Marmots are facultatively social and form harem-polygynous matrilines: mother–daughter–sister groups (Armitage, 2014). Matrilines are typically composed of one or two females defended by a territorial adult male (Armitage & Schwartz, 2000). Social groups are composed of one or more adult males and females (>2 years old), yearlings (1 year old) and pups (<1 year old) (Downhower & Armitage, 1971). Although social groups may have several adult males, only one is dominant (Armitage, 2007).

Ethical Note

Marmots were studied under the University of California, Los Angeles Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and under permits from the Colorado Division of Wildlife (TR917, renewed annually). Marmots were live-trapped and marked to facilitate observations. Traps were set in the morning and late afternoon (only when it was cool) and checked within 2 h of setting. Trapped marmots were processed quickly (within 5–15 min depending upon what needed to be done) and released at the point of capture. Prior work revealed that only individuals that struggle in a trap (relatively few of them) show an increased glucocorticoid response (Smith et al., 2012). The vast majority of trapping events involved relaxed individuals. These methods have been used for 61 years at the study site with no detectable effect on population viability.

Quantifying Behavioural Interactions

We observed individually identified, free-living yellow-bellied marmots during their active season (mid-April to early September), during hours of peak activity (from 0700 to 1000 hours in the morning and 1600 to 1900 hours in the afternoon) (Blumstein et al., 2009) between 2002 and 2019. For this study, however, we considered only observations conducted from mid-April to mid-June. We focused on this period to avoid confounding effects on the topological knockout experiments because, after mid-June, group membership changes naturally due to dispersal of yearlings and birth of pups. Observers recorded all marmots' social interactions following an all-occurrence sampling scheme (details in Wey & Blumstein, 2010). For each interaction, observers recorded the initiator, the receiver, the type of interaction (i.e. affiliative or agonistic), time of observation and location.

Definition of Social Groups

Social groups are composed of two or more individuals that live in close proximity. Here, we define our social groups as 'colonies' because these individuals co-occur in geographically distinct areas between which there is virtually no social contact or spatial overlap within years. Because groups vary in size and composition between years, we defined groups for each year of the study (i.e. group-year). We filtered our data by eliminating any marmot observed fewer than five times per year so as to eliminate transient individuals. We focused on nine geographically distinct areas (Avalanche, Boulder, Bench-River, Cliff, Gothic Town, Horse Mound, Marmot Meadow, North Picnic and Picnic), and on colonies composed of five or more interacting individuals and containing at least one adult (i.e. ≥2 years old) male and one adult female. On average, groups were composed of 53% yearlings (60% females, 40% males) and 47% adults. In total, our data comprised 60 group-years for the affiliative networks and 49 group-years for the agonistic networks, because agonistic interactions are less commonly observed and fewer networks fulfilled the above criteria.

Social Network Measures

Social network analysis considers groups in terms of the social relationships (links) that connect individual group members (nodes), including indirect connections. Thus, beyond dyadic interactions, it views societies as heterogenous, polyadic networks and provides the possibility to derive a set of metrics for sociality that are clearly defined and statistically quantifiable (Wasserman & Faust, 1994). Social network analysis distinguishes between node level metrics, which focus on individuals' positions within a given network, and network level metrics, which consider the overall network. Node level metrics can be related to individual attributes such as age, sex, body size, etc., to examine how such intrinsic factors affect individual social positions (e.g. Archie et al., 2006; Bergman & Moore, 2003; Sosa, 2016; Wey & Blumstein, 2010). Node level metrics may also be used to infer social roles (e.g. Sosa, 2016); however, if the focus is on network level structure, other analytic protocols such as topological knockouts may be more robust, because overall network level structure is not just the sum of node level metrics, but rather an emergent property (Blumstein, 2013; Whitehead, 2008).

For each group-year composed of at least five interacting individuals, we built affiliative and agonistic social networks in their weighted and unweighted, directed and undirected version, based on presence–absence of a link, depending on the prerequisite of the metric under investigation. Affiliative behaviour in our yellow-bellied marmot study system involves allogrooming, greeting, foraging together and sitting in close proximity (<1 m apart) or in body contact and play. Agonistic behaviour refers to interactions such as biting, aggressive chasing and displacement (detailed ethogram in Wey & Blumstein, 2010). Each social behaviour type was weighed the same and link weights were calculated as the sum of recoded affiliative and agonistic interactions, respectively. We calculated five global network metrics from the affiliative and agonistic networks of each social group: density, the global clustering coefficient, reciprocity, global degree centrality and the coefficient of variation of strength.

Density measures how fully a network is connected, where it considers unweighted and undirected links (Sosa et al., 2020). We calculated it as the proportion of realized networks links out of the maximum number of potential links, and its value ranges between 0 and 1.

Global clustering coefficient is a measure of group cohesion and is defined as the likelihood that any given two nodes with a common neighbour are connected themselves (Wasserman & Faust, 1994). We calculated the global clustering coefficient as the proportion of closed triplets over the total number of triplets both open and closed, and its values range between 0 and 1.

Reciprocity describes the likelihood of mutual links in a directed and unweighted network and is calculated as the ratio of the number of mutual to total links in a network. Values range between 0 and 1.

Global degree centrality assesses how much a network is dominated by a few 'popular' individuals (i.e. individuals that are linked to a relatively high number of other nodes and thus have a high local degree centrality). We calculated graph level degree centrality from node level centrality using general centralization scores (Csárdi & Nepusz, 2006). Because group size may constrain social opportunities, global degree centrality was standardized by dividing by the theoretical maximum value of the metric (Blumstein et al., 2009). As with the previous metrics, values are inherently constrained to be between 0 and 1.

Strength reflects sociality as it measures the frequency with which an individual interacts with other group members. Because strength is calculated as the sum of link weights, a high value of strength may be due to many connections with different nodes or frequent interactions with few nodes (Liao et al., 2018). We investigated the coefficient of variation (CV) of strength as a graph level index that reflects heterogeneity of node level strength within social groups. We calculated the CV of strength by dividing the standard deviation of node level strength values by its mean. In our data set, values ranged between 0.3 and 2.4.

All our calculations were conducted in the iGraph package version 1.2.7 (Csárdi & Nepusz, 2006) in R version 3.1.2 (R Core Team, 2021) and RStudio version 1.4.1106 (RStudio Team, 2021) software.

Knockout Experiments

We statistically removed nodes from our data (i.e. topological or virtual knockout) to evaluate the effect of removing an individual of a specific age–sex category from each of our social group-years. We systematically performed four removals per group-year of a single individual each: (1) a randomly selected adult male, (2) a randomly selected adult female, (3) a randomly selected yearling male and (4) a randomly selected yearling female. We then reconstructed directed and weighted social matrices and recalculated group-year size, density, the global clustering coefficient, reciprocity, global degree centrality and CV of strength from each of these knocked-out matrices.

Statistical Analysis

To account for the inherent nonindependence of social observation data and any patterns that might appear in the data due to nonsocial factors, we constructed null models for hypothesis testing (Croft et al., 2011). In a null model, the observed data are compared against a set of replicated data sets in which the factors of interest are randomized (Farine, 2017). Random data sets were constructed by permutation of the raw (‘pre-network’) data by swapping individuals of social interaction receivers within group-years. To generate the permuted networks, we first randomly swapped two receiver individuals in the original network, then we performed a swap on this first permuted network to create a second permuted network, and so forth, thus incrementally permuting networks. We repeated this 1100 times. The first 100 permuted networks were dropped (i.e. similar to a Markov chain) since permutations might still closely resemble the original sequence when only one element is modified. Thus, we considered 1000 permuted networks for each group-year. Pre-network data permutations have proved to be robust, both against type I and type II errors (Farine, 2017; Sosa et al., 2020; but see Farine & Carter, 2022; Weiss et al., 2021, for a critical discussion). We conducted data analysis in two steps: we first identified and selected the subset of group-years with networks that significantly differed from the permuted random networks (i.e. group-years were nonrandom in the sense that the observed network differed from any expected pattern under a scenario of random association between nodes), then we tested for the effects of knockouts only on the nonrandom networks.

First, and to test whether our networks were different from random with regard to a respective metric, we generated 1000 permuted interaction matrices per group-year. From these permuted matrices, we rebuilt networks and recalculated their metrics to create an expected random distribution for each of the five investigated network metrics per group-year. We then compared the observed value against its expected random distribution. Networks were considered as significantly different from random if the observed test statistic (i.e. a given metric from the observed network) fell outside the 95% confidence interval of the expected random distribution (Farine, 2017).

Second, we used a (generalized) linear mixed modelling ((G)LMM) approach to investigate whether the social structure of our groups changed after a statistical knockout. Models were fitted in R version 3.1.2 (R Core Team, 2021) and RStudio version 1.4.1106 (RStudio Team, 2021) software and analysed using the ‘glmmTMB’ package version 1.1.4 (Brooks et al., 2017). Density, global degree centrality, the global clustering coefficient and reciprocity are proportion data confined between 0 and 1. Thus, we fitted GLMMs with a beta distribution, after we transformed our response variables (y) with $(y_i \times (n-1)+0.5)/n$ where n is the sample size (Smithson & Verkuilen, 2006), as it included values of 0 and 1. The density model for the affiliative networks and the clustering model for the agonistic networks had issues with misspecification of the distribution as indicated by the KS test; thus, we refitted them with a Tweedie distribution, an exponential dispersion model (Dunn & Smyth, 2008), which resolved issues. The variable CV strength is positive but does not have an upper limit. Thus, we initially modelled CV strength as a gamma regression, but because the model did not converge, we resorted to a linear mixed model and square-root transformation of CV strength. Fitting Gaussian models to non-normal data yields more robust models and leads to more reliable *P* values (Knief & Forstmeier, 2021).

Data were grouped by group and year. Because groups vary dramatically each year due to natural processes (birth, death, dispersal), we modelled this grouping of the data as an observation level random intercept ‘group-year’. Separate models were fitted for each the five investigated metrics. Knockout condition was included as a fixed factor with five levels: (1) original network, (2) adult male knockout, (3) adult female knockout, (4) yearling male knockout and (5) yearling female knockout. Group size is known to affect social structuring in yellow-bellied marmots (Maldonado-Chaparro et al., 2015). Thus, the models included group size that year as a covariate. Furthermore, we allowed for nonlinear relationships between group size and the respective metrics by testing for second-order polynomial and logarithmic effects of group size (Maldonado-Chaparro et al., 2015). Nonlinear effects were selected based on the Akaike's information criterion (AIC; Akaike, 1973). Lastly, group size was centred to its mean for a more meaningful interpretation of the model intercept.

For beta models, estimates were backtransformed from the logit scale (the canonical link function of beta regression) by exponentiating to obtain odds ratios (OR), which describe the change in odds of the response for a one-unit increase in a continuous predictor or, for a categorical predictor, the change in odds of the response from a baseline value to each of the categories. Intercepts were backtransformed with the inverse logit and can be interpreted as the average response (original scale) when all predictors are zero. Estimates in Tweedie models were backtransformed from the log scale (the canonical link function of Tweedie models) by exponentiating; estimates of the CV strength model for affiliative network were backtransformed to the original scale by raising to the power of two.

Model diagnostics were conducted using the ‘DHARMa’ package version 0.4.4 (Hartig, 2021), focusing on the *Q*–*Q* plot (observed versus expected values), KS, dispersion and outlier tests and quantile deviations (residuals versus predicted values). Multicollinearity was tested by checking the variance inflation factor (VIF) using the ‘car’ package version 3.0.11 (Fox et al, 2019). Wald's method was used for computing degrees of freedom, standard errors and confidence intervals in the ‘sjPlot’ package version 2.8.11.4 (Lüdecke, 2022).

RESULTS

We constructed 60 affiliative and 49 agonistic social networks based on 16 579 affiliative interactions observed from 735 unique individuals and 3131 agonistic interactions observed from 660 unique individuals, where an individual was observed during an average (± SD) of 0.4 ± 2.7 affiliative and 0.1 ± 0.7 agonistic interactions.

All of the affiliative and agonistic networks were structured nonrandomly with regard to global degree centrality, CV strength and density, while only a subset of the investigated networks were nonrandom with regard to clustering (affiliative: 48 out of 60 networks; agonistic: 29 out of 49) and reciprocity (affiliative: 59 out of 60; agonistic: 32 out of 49). Average (± SD) group size was 22 ± 13 animals in the affiliative networks and 23 ± 13 animals in the agonistic networks.

Group size was negatively associated with the explored metrics both in the affiliative and agonistic networks, except for CV strength, which was always positively related to group size. These trends are consistent with previous findings reporting a similar constraint on yellow-bellied marmot relationships (Maldonado-Chaparro et al., 2015).

The knockout experiments (example in Fig. 1) show that individuals from different age–sex categories play specific roles in shaping group social structure. Yearling removals, irrespective of sex, led to significant changes in the affiliative group structure with respect to group cohesion (i.e. clustering), general connectivity (i.e. density) and reciprocity. Adult males were central actors in agonistic networks, whereas adult female removal had no effect in affiliative or agonistic networks (Tables 1–2, Fig. 2).

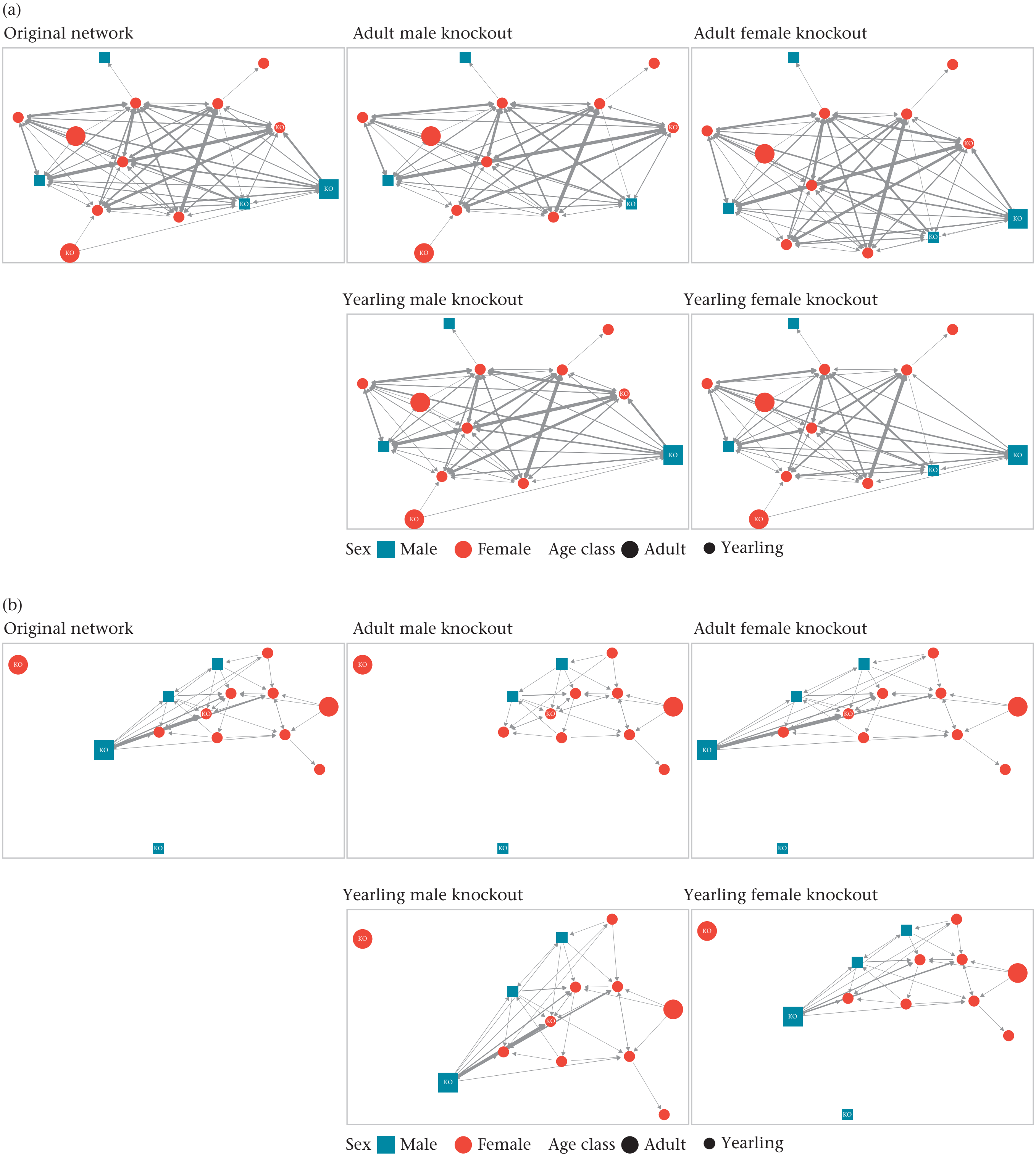

Figure 1. Illustration of how a yellow-bellied marmot social network changes as a result of adult/yearling male/female knockout in (a) affiliative and (b) agonistic networks. In the graphs, social interactions are represented by links (i.e. lines) and individuals of different age–sex categories are represented by nodes. Shape, shading and size of the nodes correspond to the following age–sex categories: large blue square (adult male); large red circles (adult female); small blue square (yearling male); small red circle (yearling female). Examples of knockout nodes are labelled ‘KO’. Depicted is the colony-year Avalanche 2013.

Table 1

Knockout effects on affiliative networks

	Density			Global clustering			Reciprocity			CV strength			Global degree centrality		
	Estimate	CI	*P*	Odds ratio (OR)	CI	*P*	OR	CI	*P*	Estimate	CI	*P*	OR	CI	*P*
Predictors															
(Intercept)	0.17	0.15, 0.20	**<0.001**	0.63	0.58, 0.68	**<0.001**	0.70	0.64, 0.75	**<0.001**	1.0815	1.0042, 1.1616	**<0.001**	0.19	0.17, 0.22	**<0.001**
Group size	0.40	0.32, 0.50	**<0.001**	0.56	0.40, 0.80	**0.001**	0.60	0.41, 0.89	**0.011**	0.0151	0.0039, 0.0338	**<0.001**	0.98	0.97, 0.99	**<0.001**
AdMKO	0.92	0.88, 0.96	**<0.001**	1.06	0.91, 1.24	0.437	1.02	0.91, 1.14	0.751	0.0004	0.0000, 0.0013	**0.011**	0.96	0.87, 1.05	0.329
AdFKO	0.98	0.95, 1.02	0.416	0.98	0.84, 1.15	0.825	1.01	0.90, 1.13	0.928	0.0000	0.0003, 0.0002	0.870	0.97	0.88, 1.06	0.455
YrMKO	0.90	0.87, 0.94	**<0.001**	0.81	0.70, 0.95	**0.009**	0.87	0.77, 0.97	**0.015**	0.0002	0.0000, 0.0009	0.075	0.95	0.87, 1.05	0.316
YrFKO	0.90	0.86, 0.93	**<0.001**	0.90	0.77, 1.05	0.171	0.83	0.74, 0.93	**0.001**	0.0003	0.0000, 0.0011	**0.025**	0.95	0.87, 1.05	0.321
Random effects															
σ^2	0.01			−0.01			−0.01			0.0018			0.03		
$\tau_{00\text{colony\_year}}$	0.31			0.46			0.83			0.0204			0.26		
ICC	0.97			1.03			1.01			0.9187			0.89		
$N_{\text{colony\_year}}$	60			48			59			60			60		
Observations	298			238			293			298			298		
Marginal R^2	0.480			0.201			0.107			0.1943			0.170		
Conditional R^2	0.984			1.021			1.011			0.9345			0.907		

AdMKO: adult male knockout; AdFKO: adult female knockout; YrMKO: yearling male knockout; YrFKO: yearling female knockout. Significant effects are shown in bold.

Table 2

Knockout effects on agonistic networks

	Density			Global clustering			Reciprocity			CV strength			Global degree centrality		
	Odds ratio (OR)	CI	*P*	Estimate	CI	*P*	OR	CI	*P*	Estimate	CI	*P*	OR	CI	*P*
Predictors															
(Intercept)	0.14	0.12, 0.17	**<0.001**	0.48	0.44, 0.54	**<0.001**	0.69	0.57, 0.82	**<0.001**	1.21	1.14, 1.28	**<0.001**	0.20	0.17, 0.23	**<0.001**
Group size	0.25	0.19, 0.33	**<0.001**	0.98	0.97, .98	**<0.001**	0.98	0.97, 0.99	**0.007**	0.40	0.30, 0.51	**<0.001**	0.60	0.47, 0.76	**<0.001**
AdMKO	0.82	0.76, 0.90	**<0.001**	0.98	0.93, 1.03	0.339	0.86	0.77, 0.97	**0.016**	0.00	−0.04, 0.04	0.932	0.80	0.72, 0.88	**<0.001**
AdFKO	0.95	0.87, 1.03	0.214	0.97	0.92, 1.02	0.220	1.04	0.92, 1.17	0.509	0.04	−0.00, 0.08	0.069	1.00	0.91, 1.09	0.962
YrMKO	0.89	0.81, 0.97	**0.006**	0.98	0.93, 1.03	0.329	0.96	0.85, 1.08	0.505	0.03	−0.01, 0.07	0.104	0.97	0.88, 1.06	0.487
YrFKO	0.91	0.84, 0.99	**0.037**	0.96	0.91, 1.01	0.091	0.93	0.82, 1.05	0.218	0.03	−0.01, 0.07	0.133	0.96	0.87, 1.05	0.384
Random effects															
σ^2	0.03			0.01			0.01			0.01			0.03		
$\tau_{00\text{colony\_year}}$	0.32			0.07			0.20			0.05			0.25		
ICC	0.91			0.88			0.97			0.84			0.89		
$N_{\text{colony\_year}}$	49			29			32			49			49		
Observations	237			143			157			242			242		
Marginal R^2	0.651			0.577			0.206			0.492			0.255		
Conditional R^2	0.969			0.951			0.974			0.916			0.915		

AdMKO: adult male knockout; AdFKO: adult female knockout; YrMKO: yearling male knockout; YrFKO: yearling female knockout. Significant effects are shown in bold.

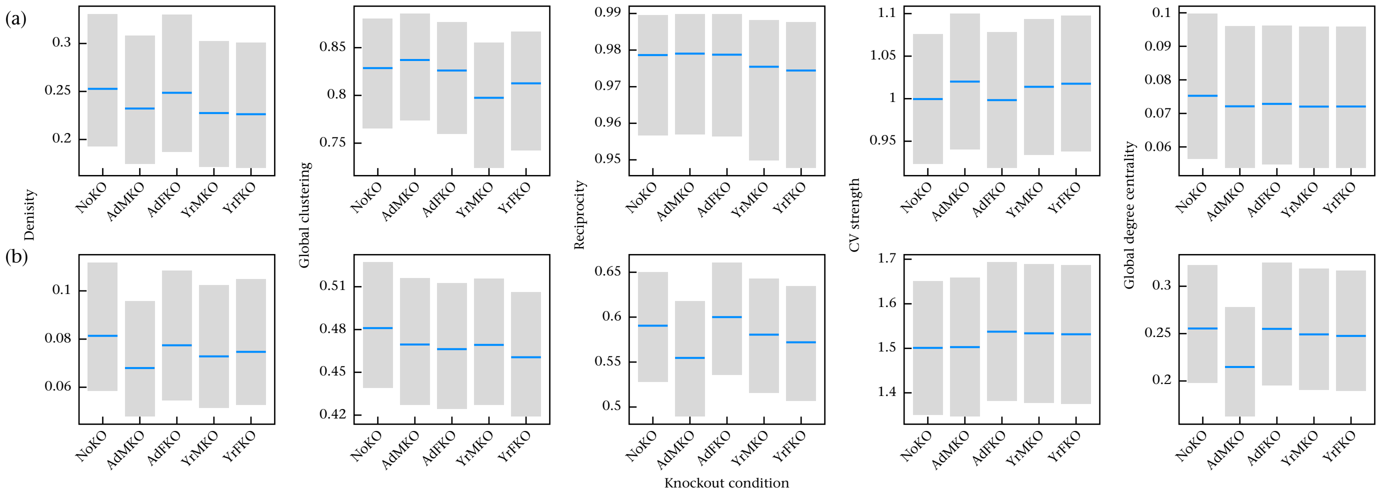

Figure 2. Marginal relationships of knockout condition in (a) affiliative and (b) agonistic networks, with mean values (blue lines) of the five investigated network metrics: density, global clustering coefficient, reciprocity, coefficient of variation (CV) of strength and global degree centrality. Grey shaded areas show 95% confidence intervals. NoKO: original networks; AdMKO: adult male knockout; AdFKO: adult female knockout; YrMKO: yearling male knockout; YrFKO: yearling female knockout.

Knockout Effects on Affiliative Networks

A knockout of any age–sex category, except for the adult female removal, reduced density in affiliative networks. Because density measures overall connectedness, we infer from this that the loss of a group member generally disrupts the social structure. Yearling knockouts, both male and female, had a slightly greater effect on global network structure. The yearling male knockout decreased density an average of 10% (estimate = 0.90; confidence interval, CI = 0.87–0.94), which corresponds to a mean density of 0.227 (CI = 0.171–0.302) in the yearling male knockout network, as compared to a mean density of 0.253 (CI = 0.193–0.331) in the original network (Table 1, Fig. 2). Similarly, the yearling female knockout decreased density an average of 10% (estimate = 0.90; CI = 0.86–0.93), corresponding to a mean density of 0.226 (CI = 0.179–0.301), while adult male knockout decreased density an average of 8% (estimate = 0.92; CI = 0.88–0.96), corresponding to a mean density of 0.232 (CI = 0.175–0.310) in the adult male knockout network. Adult female knockout had no effect (estimate = 0.98; CI = 0.95–1.02). Male yearlings seem to be major actors in affiliative networks and were particularly important in maintaining group cohesion: The regression coefficient for yearling male knockout on global clustering returned an odds ratio (OR) of 0.81 (CI = 0.70–0.95), suggesting that yearling male knockout was associated with a 19% lower odds of global clustering, which corresponds to a mean clustering coefficient of 0.797 (CI = 0.724–0.855) in the yearling male knockout network as compared to a mean clustering coefficient of 0.829 (CI = 0.764–0.878) in the original network. Moreover, yearling male knockout as well as yearling female knockout were associated with an average of 13% (CI = 0.77–0.97) and 17% (CI = 0.74–0.93) lower odds of reciprocity, respectively, corresponding to mean reciprocities of 0.975 (CI = 0.950–0.988) and 0.974 (CI = 0.947–0.987) in the yearling male knockout and yearling female knockout networks, as compared to a mean reciprocity of 0.979 (CI = 0.957–0.990) in the original network. Degree centrality was not modified by knockout in the affiliative networks. CV strength increased with yearling female knockout (estimate = 0.0003; CI = 0.0000–0.0011) and adult male knockout (estimate = 0.0004; CI = 0.0000–0.0013), but the effect size was low. Thus, yearlings and adult males play distinct roles in marmot affiliative social networks, whereas adult females seem less important with regard to the investigated metrics.

Knockout Effects on Agonistic Networks

Like the affiliative networks, agonistic networks were generally disrupted by knockout, except for by the adult female knockout, as evident by comparably lower odds of density in this condition as compared to the original networks. Adult male knockout was associated with 18% lower odds of density as compared to the original network (OR = 0.82; CI = −0.76–0.90), which corresponds to a mean density of 0.068 (CI = 0.048–0.096) in the adult male knockout network as compared to a mean density of 0.081 (CI = 0.059–0.112) in the original network (Table 2, Fig. 2). Yearling male knockout was associated with 11% (OR = 0.89; CI = 0.81–0.97) and the yearling female knockout with 9% (OR = 0.91; CI = 0.84–0.99) lower odds of density as compared to the original network, which corresponds to a mean density of 0.073 (CI = 0.051–0.102) in the yearling male knockout and a mean density of 0.075 (CI = 0.053–0.105) in the yearling female knockout. Adult males seem to be the main agents structuring agonistic relationships. Besides density, adult male knockout was associated with distinctly lower odds of degree centrality by an average of 20% (OR = 0.80; CI = 0.72–0.88), which corresponds to a mean degree centrality of 0.215 (CI = 0.163–0.278) in the adult male knockout network as compared to 0.255 (CI = 0.200–0.322) in the original network. Moreover, adult male knockout was associated to lower odds of reciprocity by an average of 14% (OR = 0.86; CI = 0.77–0.97), corresponding to a mean reciprocity of 0.555 (CI = 0.490–0.618) as compared to a mean reciprocity of 0.590 (CI = 0.528–0.650) in the original network. Clustering and CV strength were not affected by knockout condition. As in the affiliative networks, adult female knockout did not affect any of the investigated metrics. Thus, adult females may not play a major role in the structure of agonistic networks.

DISCUSSION

Based on a systematic exploration of simulated removals, we show that the social networks of free-living yellow-bellied marmots structurally respond to altered group composition and, thus, may be shaped by demographic processes. Previous studies of other species have mostly focused on the effects of targeted (virtual or experimental) removals of specific key individuals, often dominant group members or otherwise most central individuals (e.g. Flack et al., 2006; Goldenberg et al., 2016; Lusseau, 2003), or the random removal of a larger number of group members (e.g. Firth et al., 2017; Testard et al., 2021). In contrast, our simulated knockouts provide a more general investigation into the effects of demographic roles on social networks. Our results show not only that specific key individuals matter in shaping social structure, but also that animals from different age–sex categories have distinct roles in their social groups. These results are consistent with our initial hypotheses and show that the consequences of losing a group member varies based on their demographic role. In marmots, yearlings and yearling males, in particular, are major actors in shaping affiliative networks and maintaining group cohesion, while adult males are the central players in agonistic relationships.

The removal of certain individuals led to structural changes in marmot social networks, which we infer could then subsequently alter social relationships such as dominance or cooperation (Hemelrijk, 1999), information flow (McComb et al., 2001), pathogen transmission (Keeling & Eames, 2005), mating or predator avoidance (Croft et al., 2008). This is because the development of such relationships is shaped by the group's social structure (Sundaresan et al., 2007). Thus, we expect that changes in social structure matter because they may impact individual fitness and population dynamics (Anthony & Blumstein, 2000; Cantor et al., 2021; Gerber et al., 2022; Snijders et al., 2017).

Network density, a basic measure of social connectivity, decreased with the removal of an individual of any age–sex category except for adult females in the agonistic and affiliative networks. Social animals must balance costs and benefits of sociality (Armitage, 2014; Silk, 2007), and social groups should maintain (more or less) stable configurations that are adaptive in the prevailing environment and under given constraints (Hinde, 1976; Shultz et al., 2011). For marmots, previous studies have shown that individuals can adjust their social behaviour to potentially optimize this trade-off in different environments (Maldonado-Chaparro et al., 2015). Thus, if we assume that established groups have achieved some sort of stable optimum, changes in the existing social structure may be understood as a disturbance of this stability and this may have group level costs (Firth et al., 2017; Maldonado-Chaparro et al., 2018).

Yearling knockouts decreased social connectivity independent of sex. This finding is in line with our hypothesis and with previous studies showing that yearlings are more interactive than adults and, thus, highlights the role of yearlings as connecting elements of marmot social groups (Wey & Blumstein, 2010). However, on a finer scale, male and female yearlings contributed differently to the overall network structure. Yearling males seem particularly important in maintaining cohesion in affiliative networks (as indicated by the negative effect of yearling male knockout on the global clustering coefficient). High clustering in yellow-bellied marmots' social networks may facilitate the transmission of information and disease. In social groups, direct contact among individuals in the group facilitates pathogen transmission (Altizer et al., 2003); therefore, if individuals are highly clustered, diseases could potentially spread rapidly throughout the group. Likewise, information about the location of resources such as food or predators could easily be transmitted throughout the network (Farine & Whitehead, 2015; Galef & Laland, 2005). For example, in ungulates, information about resources is transmitted from knowledgeable individuals to naïve individuals by copying (Galef & Laland, 2005).

High clustering in marmots can also promote the development of reciprocal relationships, such as mutual grooming, as has been suggested for Grevy's zebra, *Equus grevyi* (Sundaresan et al., 2007), and dolphins (Lusseau & Newman, 2004). Importantly, yearling male yellow-bellied marmots played a central role in maintaining reciprocal (i.e. mutual) relationships within their group. Similarly, although yearling females contributed to network reciprocity, they contributed less to network cohesion (as simulated loss of yearling females did not affect clustering of the affiliative networks). This was somewhat surprising since almost all male yearlings disperse, whereas about half of yearling females remain in their natal group (Blumstein et al., 2009).

While yearlings shaped affiliative relationships, adult males were the central elements in agonistic networks (as indicated by the strong negative relation between adult male knockout and degree centrality), their removal decreased agonistic social connectivity by about 50% more than that seen when a yearling was removed. This central role might be related to male reproductive strategies and, as predicted, by their effort to monopolize one or several matrilines. In marmots, adult males increase reproductive success by establishing a territory from which they exclude competitors though agonistic interactions (Armitage, 2014). Adult males also seem to play a socially integrative role since adult male removal led to increased heterogeneity in individual strength of social relationships in affiliative networks. This may be because specific individuals preferentially maintain relationships with adult males. For example, adult males must maintain amicable relationships with adult females to secure reproductive opportunities (Armitage, 1998) and yearlings often direct interactions towards the dominant male, which is usually their father (Armitage, 2014). Less intuitively, yearling females also seem to have a similar integrative function, but this may be because they are socially embedded in their group, a social attribute that has been associated with a reduced likelihood of dispersal (Blumstein et al., 2009).

In contrast to yearlings and adult males, adult females seem to play a minor role in shaping the group structure with regard to the investigated metrics; simulated female loss did not significantly affect any of the investigated metrics in affiliative or agonistic networks. This finding was unexpected because yellow-bellied marmot females are the ‘backbone’ of matrilines. Adult females maintain social hierarchies and benefit from recruiting daughters into their matriline in that the presence of younger females increases survival and later reproduction of offspring (Armitage, 1986).

Because social cohesion is a major predictor of dispersal in yearling female yellow-bellied marmots (Armitage, 2014; Blumstein et al., 2009), we would expect that adult females are more relevant in shaping network structure in this respect. Yet, sociality is also costly because of reproductive suppression, which is directed from the dominant female to younger subordinates, including daughters, through agonistic interactions (Armitage, 1986). Moreover, previous studies have shown that affiliation strength is negatively related to annual reproductive success in yellow-bellied marmot females (Wey & Blumstein, 2012).

Subdominant females, which may be reproductively suppressed, may disperse or avoid agonistic encounters, or engage in preferential relationships to reduce female–female competition; that is, they may maintain a few high-quality relationships rather than many lower-quality relationships (Dakin & Ryder, 2020; Lehmann & Boesch, 2009; Oli & Armitage, 2003). Our results indicate that yearling females may indeed engage in high-quality relationships that are also predominantly reciprocal, a characteristic of high-quality relationships (Dakin & Ryder, 2020). This exclusivity in social relationships was not observed for adult females. Thus, the lack of adult females contributing to graph level reciprocity may result from reproductive competition between adults (Armitage, 2014). If adult females spatially avoid other females to reduce competition, then this would also decrease space overlap and thus opportunities for social interactions with other conspecifics (Barrat et al., 2005; Pinter-Wollman et al., 2014). This hypothesis must be formally tested with more detailed spatial analyses.

Our finding that different age–sex classes contribute differently to network structure aligns with various studies that have reported how individual attributes such as age and sex, but also personality or kinship, are related to network position (e.g. Blumstein et al., 2009; Croft et al., 2004, 2005; Wey & Blumstein, 2012; Williams & Lusseau, 2006). In some social systems, key players are vital for network structure and network level processes, such as the flow of information (Flack et al., 2006; Lusseau & Newman, 2004; Pinter-Wollman et al., 2011), where key players are often individuals of a specific age–sex class, depending on the species (Flack et al., 2006; Lusseau & Newman, 2004; McComb et al., 2001). In yellow-bellied marmots, the general importance of yearling males in shaping social structure and cohesion and the minor role of adult females is somewhat surprising, because yearling males are the ones that almost certainly disperse. This finding, in particular, stimulates more questions about their role in marmot societies and how this connectivity provides social information that may influence their dispersal decisions.

In a real-world scenario, networks may be reconfigured through behavioural adjustment of individuals, which may buffer the effect of changes in group composition (Goldenberg et al., 2016). Yet, behavioural adjustment may be costly. For example, in zebra finches, *Taeniopygia guttata*, the temporary splitting of flocks decreases group-foraging efficiency after reunion (Maldonado-Chaparro et al., 2018) and, more generally, stress and social behaviour are deeply intertwined (Beery & Kaufer, 2015; Blanchard et al., 2001). Additionally, costs may depend on the level of the structural disturbance, and this can be highlighted with a topological knockout approach. This idea remains to be tested by complementing the statistical removal of individuals with an experimental approach and by quantifying changes in stress levels and fitness-related behaviours in response to a knockout. However, it is important to realize that because of their social plasticity and the relatively few identified benefits of sociality, yellow-bellied marmots may be more resilient to the loss of individuals than other, more obligately social species. Again, this hypothesis remains to be tested by studying other species using similar techniques.

Together, our results illustrate how simple demographic processes (the loss of single individuals from different age–sex categories) generate structural variation in the social structure of a free-living rodent. Importantly, the consequences of losing a group member are expected to depend on age- and sex-specific roles. In marmots, yearling males play a relatively large role in shaping the structure of affiliative and agonistic networks despite the fact that they will almost certainly disperse. Ultimately, knowledge of demographic roles as well as the loss of specific roles and their potential consequences on social structure provides valuable information that can help identify the situations under which anthropogenic impacts on wildlife population demography are of concern and thus guide wildlife management.

Author Contributions

D.T.B. and A.M.C. conceived the ideas, designed methodology and contributed to data collection. A.M.C., D.T.B. and F.Z. analysed the data. A.S. and S.G. contributed to data preparation and wrote an initial preliminary draft. A.M.C., D.T.B. and F.Z. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability

Data and code to replicate the analyses are available at OSF at https://osf.io/yrhnc/?view_only=3ad4065d693b4bbca497f00651983690.

Declaration of Interest

None.

Acknowledgments

This work was supported by the National Geographic Society, UCLA (Faculty Senate, the Division of Life Sciences and the Department of Ecology and Evolutionary Biology), the U.S. National Science Foundation (I.D.B.R.-0754247, D.E.B.-1119660 and 1557130 to D.T.B.; D.B.I. 0242960, 0731346 and 1226713 to the Rocky Mountain Biological Laboratory). F.Z. was supported by a scholarship of the German Federal Environmental Foundation (Deutsche Bundesstiftung Umwelt DBU; 20021/724).

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