ISSN 1465-7279 (ONLINE)

The official journal of the
International Society for Behavioral Ecology

Behavioral Ecology

VOLUME 33 NUMBER 1 JANUARY/FEBRUARY 2022

https://academic.oup.com/beheco



Downloaded from https://academic.oup.com/beheco/issue/33/1 by University of California, Los Angeles user on 21 February 2022

OXFORD
UNIVERSITY PRESS

Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2022), 33(1), 115–125. https://doi.org/10.1093/beheco/arab114

Original Article

Marmot mass gain rates relate to their group's social structure

Conner S. Philson,[a,b,*] Sophia M. Todorov,[a,*] and Daniel T. Blumstein[a,b]

[a]Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095–1606, USA and [b]Rocky Mountain Biological Laboratory, Box 519, Crested Butte, CO 81224, USA

Received 20 January 2021; revised 1 September 2021; editorial decision 16 September 2021; accepted 23 September 2021; Advance Access publication 20 October 2021.

Mass gain is an important fitness correlate for survival in highly seasonal species. Although many physiological, genetic, life history, and environmental factors can influence mass gain, more recent work suggests the specific nature of an individual's own social relationships also influences mass gain. However, less is known about consequences of social structure for individuals. We studied the association between social structure, quantified via social network analysis, and annual mass gain in yellow-bellied marmots (*Marmota flaviventer*). Social networks were constructed from 31 738 social interactions between 671 individuals in 125 social groups from 2002 to 2018. Using a refined dataset of 1022 observations across 587 individuals in 81 social groups, we fitted linear mixed models to analyze the relationship between attributes of social structure and individual mass gain. We found that individuals residing in more connected and unbreakable social groups tended to gain proportionally less mass. However, these results were largely age-dependent. Adults, who form the core of marmot social groups, residing in more spread apart networks had greater mass gain than those in tighter networks. Yearlings, involved in a majority of social interactions, and those who resided in socially homogeneous and stable groups had greater mass gain. These results show how the structure of the social group an individual resides in may have consequences for a key fitness correlate. But, importantly, this relationship was age-dependent.

Key words: **fitness consequences, mass gain, network density, social homophily, social network analysis, social structure.**

INTRODUCTION

Body condition is an index of an individual's phenotypic quality and is often an important fitness correlate (Schulte-Hostedde et al. 2001; Milner et al. 2003). One measure of body condition is an individual's relative amount of energy storage, often quantified as body fat accumulation (Green 2001). Previous work has used such indices to identify the consequences of body condition for reproductive success (Chastel et al. 1995; Testa and Adams 1998) and survival (McMahon et al. 2000; Burton et al. 2006). For example, female polar bears (*Ursus maritimus*) with greater fat stores are able to produce heavier cubs that are more likely to survive (Atkinson and Ramsay 1995). A similar relationship is also present in canvasbacks (*Aythya valisineria*), a species in which body mass and fat reserves are highly correlated, where individuals with greater winter mass experienced higher overwinter and annual survival (Haramis et al. 1986). In adults of many species, an increase in body mass is largely a function of fat accumulation, and thus body mass serves as a good measure to quantify fat accumulation (Stevenson and Woods 2006).

Body mass is especially important in preparation for major life history events (Blem 1980; Klaassen and Biebach 1994). Energy reserves are necessary before migration, for example, because individuals are unable to stop and forage for long periods of time while migrating and thus rely heavily on reserves (Bairlein 2002). Therefore, individuals must change their foraging behavior to rapidly increase body mass pre-migration (Pennycuick 1975; Masman and Klaassen 1987; Dunn 2002). However, mass gain before a life history event can result in a trade-off between time spent feeding and time allocated to other important activities, such as anti-predator behavior (Metcalfe and Furness 1984). Migratory birds may also experience physiological trade-offs to maintain maximum fat reserves; such is the case for the common snipe (*Gallinago gallinago*), which delay their first post-juvenile molt (an energetically costly event) to avoid overlap with migration (Podlaszczuk et al. 2016).

Similar to migration, though with different physiological drivers, fat reserves serve as the primary source of metabolic energy during periods of hibernation (Dark 2005). However, too much body fat too early before hibernation may be unfavorable, potentially preventing individuals from escaping predators or reproducing (Bachman 1993; Clark and Dukas 1994). Therefore, having adequate body fat to survive hibernation can be a complex trade-off between maintaining

*These authors are the co-first authors.
Address correspondence to C.S. Philson. E-mail: cphilson@ucla.edu.

© The Author(s) 2021. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology.
All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

moderate body mass in the active months while also possessing sufficient fat reserves to last hibernation (Armitage et al. 2007; Willis 2017). As a result, many species undergo rapid physiological changes in a short time before hibernation, such as increasing fat storage via above-average food consumption (Lyman and Chatfield 1955). This increased storage and consumption can be measured by a high rate of mass gain (Armitage et al. 1976; Kiell and Millar 1978). In some species, the rate of mass gain can be used as a predictor of over-winter survival, with individuals who undergo rapid mass gain leading up to hibernation experiencing higher over-winter survival (Lenihan and Vuren 1996; Blumstein et al. 2016). Therefore, because body mass is an important fitness correlate, it is important to understand what influences mass gain.

Mass gain is mediated by both internal and external factors. Internal factors may include individual metabolic rate (French 1985), age (Millesi et al. 1999), body size (Armitage et al. 2003), and sex (Cameron and Spencer 1983), which have been shown to influence the rate of food acquisition, digestion, and storage in a variety of mammals. External factors may include environmental variation (Maldonado-Chaparro et al. 2015b), the number of young to care for (Allainé et al. 1998), predator pressure distracting from foraging (Pérez-Tris et al. 2004), relative level of interspecific (Harris and Macdonald 2007) and intraspecific competition (Amir et al. 2000), and indirect genetic effects (Rauter and Moore 2002). Although this work has begun to explore many internal and external factors, the relationship between social interactions and mass gain rates is understudied.

Social interactions may have both negative and positive fitness consequences (Rubenstein 1978; Krause and Ruxton 2002; Majolo et al. 2008; Chapman and Valenta 2015; Markham and Gesquiere 2017). In some situations, costs may include increased pathogen and parasite transmission (e.g., bighorn sheep, *Ovis canadensis*; Côté and Poulinb 1995; Manlove et al. 2014), increased attraction of predators (e.g., elk, *Cervus elaphus*; Hebblewhite and Pletscher 2002), and higher intraspecific competition for resources (e.g., pholcid spiderlings, *Holocnemus pluchei*; Jakob 1991). However, sociality need not be detrimental. Benefits may include protection from predators (e.g., Alaskan moose, *Alces alces gigas*; Molvar and Bowyer 1994; white-nosed coatis, *Nasua narica*; Hass and Valenzuela 2002), higher reproductive success (e.g., prairie voles, *Microtus ochrogaster*; Solomon and Crist 2008), enhanced resistance or tolerance to parasites (e.g., leaf-cutting ants, *Acromyrmex echinatior*; Hughes et al. 2002; Ezenwa et al. 2016), and information sharing (Safi and Kerth 2007). Another benefit of sociality is increased access to food and resources (e.g., river otters, *Lontra canadensis*; Blundell et al. 2002). For example, social animals may face a decreased risk while foraging due to collective vigilance and via the selfish herd hypothesis, which could be energetically beneficial (Hamilton 1971; Lovegrove and Wissel 1988). This link between sociality and food acquisition suggests the nature and frequency of one's social interactions may also be an important factor for mass gain.

As an example of the potential sociality-mass gain relationship, more social capuchin monkeys (*Cebus apella*) have greater access to known food resources and are better able to locate and access novel sources (Galloway et al. 2005; Dindo 2009). In zebra finches (*Taeniopygia guttata*), females that feed with more companions have better body condition (Crino et al. 2017). Moreover, banded geckos (*Coleonyx variegatus*) who aggregate increase their access to resources (Lancaster et al. 2006). These works have shown how variation in individual sociality can be an important factor explaining variation

Table 1
Network-level measures used to quantify social structure along with the hypothesized direction of the relationship between the social measure and mass gain rate

Measure	Description	References	Interpretation	Hypothesis
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 connected and cyclical a group is	+
Reciprocity	The number of mutual interactions divided by the number of possible mutual interactions	Wasserman and Faust 1994; Kankanhalli et al. 2005; Squartini et al. 2013	How mutual 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 degree	+
Diameter	Path length between the two most distant nodes	Watts and Strogatz 1998; Broder et al. 2000	Identifies the size of a network, in addition to raw group size	–
Cut points	Number of social ties that must be cut to create two separate networks.	Wasserman and Faust 1994; Borgatti 2006	How stable or fragmentable a group is	–
Centralization	Extent to which a network is dominated by one or few nodes.	Freeman 1979; Wasserman and Faust 1994; Kang 2007	Identifies if most social interactions in a group flow through one or few individuals (e.g., star network)	+

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

in body condition and potential for increased mass gain, though more empirical studies are needed.

Although many previous studies have identified a relationship between individual sociality and fitness (Rubenstein 1978; Krause and Ruxton 2002; Majolo et al. 2008; Chapman and Valenta 2015; Solomon-Lane et al. 2015; Markham and Gesquiere 2017), less empirical work has focused on the fitness consequences of social structure – the pattern of all social interactions in group. This gap in the animal social network literature is especially true when considering the individual mass gain in hibernating species. That is, how does a group's social structure affect each individual in that group's annual mass gain? This contrasts with prior work which explored the consequences of an individual's direct social interactions (Ratcliffe et al. 2007; Weidt et al. 2008), and not that of its entire social group. By using network-level measures derived from social network analysis (Wasserman and Faust 1994), social structure can be quantified beyond the scope of commonly used node-level measures (Farine and Whitehead 2015; Solomon-Lane et al. 2015), which describe an individual's direct relationships with others. Examining sociality at the level of the group by analyzing social structure can also provide insights into non-linear effects of sociality that may not otherwise be quantified (Kappeler 2019).

Here we used social network analysis to explore the individual mass gain-social structure interface. We used a longitudinal dataset on yellow-bellied marmots (*Marmota flaviventer*), studied in and around the Rocky Mountain Biological Laboratory (RMBL) in Colorado. Yellow-bellied marmots are obligate over-winter hibernators, relying on fat reserves acquired during an about five month (mid-April–late September) active season, though rapid mass gain occurs post-reproduction (July–September). Previous work in this system has shown both body mass (Armitage et al. 1996; Monclús et al. 2014; Blumstein et al. 2016) and annual mass gain (Maldonado-Chaparro et al. 2017; Heissenberger et al. 2020) before immergence are significant predictors of over-winter survival and the following year's reproductive success. Therefore, the population of yellow-bellied marmots at RMBL is an ideal system in which to explore the effect of social structure on individual mass gain.

Additionally, a majority of prior social network studies show that many strong social relationships are often costly for yellow-bellied marmots (reproductive success: Wey and Blumstein 2012; alarm call propensity: Fuong et al. 2015; survival: Yang et al. 2017; longevity: Blumstein et al. 2018). Thus, our a priori prediction was that individuals living in more connected social groups, which we quantified using network measures including density, transitivity, reciprocity, etc. (Table 1), would gain mass more slowly. This may be attributable to the trade-off in time allocated towards engaging in social activities versus foraging, and thus more generally captures a potential cost of sociality (Pollard and Blumstein 2008). Social interactions may also be energetically costly (Yang et al. 2017), further limiting individual mass gain in more interactive social groups.

We worked under the assumption that measures of connectivity (density and transitivity) would result in contrasting effects for mass gain rates in marmots (Table 1). Specifically, our a priori hypothesis was that density would be negatively associated with mass gain because the majority of prior social network studies in this system showed that having many individual social relationships was often costly (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018), thus suggesting more dense social structures (those with more realized relationships) will be detrimental for group residents. However, because we focused here on affiliative social networks, we also hypothesized that transitivity would be positively associated with the mass gain rate based on the finding in Wey et al. (2019) that more affiliative social groups exhibit higher rates of transitivity. We hypothesized that measures that quantified the degree to which relationships were "mutual" (reciprocity and degree assortativity) would also be positively associated with mass gain. Because agonistic interactions in yellow-bellied marmots are costly (Armitage 2014), residing in more socially mutual and homogenous groups may be beneficial. We, therefore, hypothesized a negative association between mass gain and diameter, which identifies the length of a network, as well as between mass gain and cut points, which identifies how stable or unstable a group is to fracture into two separate groups. Because the rate of individual marmot sociality plateaus as group size increases (Maldonado-Chaparro et al. 2015a), and because diameter and cut points are likely to be highly correlated with group size (Wasserman and Faust 1994), we hypothesized a negative association between them and mass gain. Lastly, we hypothesized that centralization would be positively associated with mass gain because marmots are harem-polygynous and matrilineal, suggesting groups with a central male and/or female may experience greater stability (Armitage 2014).

METHODS

Data collection

We examined the mass gain-social structure interface in the population of yellow-bellied marmots located in and 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), which have been studied continuously 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). Throughout their five-month active season from early May to mid-September, marmots must accumulate enough fat reserves to survive hibernation. Thus, they allocate a large amount of time to foraging and digesting (Armitage et al. 1996).

From 2002 to 2018, marmots were observed and repeatedly live trapped during their active season. Individuals were trapped using baited Tomahawk-live traps near burrow entrances, and immediately transferred to cloth handling bags to record body mass, sex, and age category (pups [<1 year], yearlings [=1 year], and adults [≥2 years]). Only adults are reproductively mature. All marmots were 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 a nontoxic Nyanzol fur dye (Greenville Colorants, Jersey City, NJ) to be identified from a distance. Virtually all marmots in our study population are trapped and marked annually, permitting us to accurately identify interacting individuals. For the few individuals that might lose their marks and not be recaptured after they molt, the fact that most other marmots at their respective colony site were marked, permitted us to identify them.

Marmots were studied annually at the same sites in the Upper East River Valley. Colony sites can be grouped into a higher classification of up- and down-valley (5 are up-valley, 7 are down-valley). Up-valley is at a higher elevation and experiences harsher weather conditions than down-valley (Van Vuren and Armitage 1991; Blumstein et al. 2006; Maldonado-Chaparro et al. 2015b). On sexual maturity, nearly half of females and most males disperse (Armitage 1991) with most dispersal resulting in movement out

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

of the valley. Social matrices were constructed for each group of connected individuals that appeared naturally within a valley location (up- or down-valley) and that did not interact with any other individuals.

Detailed social interactions in this population have been recorded since 2002. Behavioral observations were 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). For each interaction, we then classified the behavior 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 (81.69%) occurred between identified individuals. The initiator and/or recipient of 18.31% interactions could not be identified because the marmot's dorsal fur mark was not visible because of either the marmot's posture or visual obstructions. Excluding these interactions between unidentified individuals should not significantly influence social structure (Silk et al. 2015). Our social matrices only consisted of yearlings and adults because these cohorts were present early in the season, when social interactions are most common. We excluded pups from our matrices because most pups emerge in July and were, therefore, present only a fraction of the year. We also filtered out individuals with fewer than five interactions in a given location to eliminate those dispersing and that were not actually part of the social group (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018).

Mass gain model

To predict body masses during the growing season, we calculated best linear unbiased predictions (BLUPs) by fitting linear mixed effects models from the repeated body mass recordings taken for yearlings and adults from 2002–2018 to predict 1 June and 15 August body mass. Models were fitted in R (R Development Core Team 2020; version 3.6.3) using the "lmer" package (Bates et al. 2015; version 1.1–23). Data used in our BLUPs consisted of 7164 observations across 4077 individuals and 56 years. There was a mean of 3.4 observations per individual (range: 1.0–24.0; Median = 2.0). Martin and Pelletier (2011) showed that BLUPs can make accurate body mass predictions when there are on average greater than three measurements of body mass per individual, a criterion our data meet. The repeatability of body mass in our models varies between 0.35 and 0.47 depending on the age-sex specific model. We acknowledge that using BLUPs in follow-up analysis (such as our linear models discussed below) can lead to higher rates of Type 1 error (Hadfield et al. 2010; Houslay and Wilson 2017). However, our large dataset used to produce the BLUPs helps to mitigate this error (Dingemanse et al. 2019). Additionally, we do not use mean and mode of the posterior distribution of each BLUP after fitting in lme4 (as proposed by Hadfield et al. 2010 and Houslay and Wilson 2017) because the estimates from lme4 are equivalent. We included individual identity, year, and site as random effects in the models, producing individual- and year-specific intercept predictions (Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger et al. 2020). Therefore, to calculate individual yearling and adult proportional mass gain, we divided individual body mass on 15 August by the body mass on 1 June.

Social network measures

Using social observation data collected from 2002 to 2018 and the R package "igraph" (Csardi and Nepusz 2006; version 1.2.5), we constructed weighted and directed social interaction matrices based on observed affiliative interactions between individuals for each year. These affiliative networks consisted of 31 738 social interactions between 671 individuals in 125 social groups. 13 668 of these interactions occurred down valley and 18 068 occurred up valley. From these matrices we calculated seven social network measures to quantify social structure (described in Table 1). Our observations of marmot social groups across their entire active season and low rate of unknown individuals involved in social interactions facilitates the reliability of the seven social network measures (mean across years per individual = 33.1, range = 8.9–91.3; Supplementary Table 1; Silk et al. 2015; Davis et al. 2018; Sánchez-Tójar et al. 2018). Because some of the network measures could not be calculated for certain group sizes or group configurations (e.g., transitivity for a group of two or a linear group) and because mass gain rates could not be calculated for some individuals, we systematically removed all N/A's for network measures across all models and removed individuals without mass gain rate values. This can be attributed to some individuals only being weighed once in a year, only observed a few times a year, or due to their membership in a small group (e.g., a group of two). This final 17-year dataset used in our analysis consisted of 1022 annual observations of mass gain and group metrics, from 587 unique individuals, that lived in 81 different social groups (Supplementary Table 1).

Data analysis

To test the relationships between social structure (quantified via seven network-level measures [Table 1]) and proportional mass gain, we fitted linear mixed models in R (R Development Core Team 2020; version 3.6.3) using the "lmer" package (Bates et al. 2015; version 1.1–23). Each model had a different network measure as the primary predictor variable; mass gain was the response variable across models. All models included group size (number of individuals in a social group), number of mass recordings, sex, age, and valley location as fixed effects. We included year, individual ID, and group ID as random effects (random effects are crossed as an individual ID may be seen in multiple years, and thus in multiple group IDs across years). Categorical variables sex, age, and valley location were mean-centered following Schielzeth (2010). As such, we coded females, yearlings, and down-valley individuals as "+1" whereas males, adults, and up-valley individuals were coded as "-1.".

Group size was included as a fixed effect to account for network measures that may differ as a function of group size. The number of mass observations was included as a fixed effect to account for variation in the certainty of BLUP estimates. We included individual identity as a random effect to account for individuals that had observations over multiple years and colony ID to account for multiple members of the same group that shared a network measure within a given year. We also included interactions between the social network measure and sex, age, and valley location because these three variables are well-known correlates with mass gain; there are significant differences between the mass gain of females and males (Armitage 1998), yearlings and adults (Armitage et al. 1976), and individuals down-valley versus individuals up-valley (Van Vuren and Armitage 1991; Blumstein et al. 2006; Maldonado-Chaparro et al. 2015b).

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

Proportional mass gain rate (response variable) and the number of mass observations (predictor variable) were $\log_{10}$ transformed and all variables then were standardized (mean-centered and divided by one SD using the base "scale" function in *R*; Becker et al. 1988). We checked for collinearity by calculating correlation coefficients between continuous predictors. No models had a correlation coefficient >0.8 between the network measure and a fixed effect (Franke 2010; Shrestha 2020). After fitting each model, we calculated the marginal and conditional part R^2 values to estimate the variance explained by each of our fixed and random effects, using the "partR2" package in R (Nakagawa and Schielzeth 2013; Stoffel et al. 2021; version 0.9.1). The marginal part R^2 gives an estimate of the variance explained by each fixed effect whereas the conditional part R^2 gives an estimate of the variance explained by each fixed effect plus the variance explained by all the random effects. We estimated 95% confidence intervals for our part R^2 values using 100 parametric bootstrap iterations. Then we used the "check_model" function from the "performance" package in R (Lüdecke et al. 2020; version 0.6.1) to ensure each model met the assumptions of linear mixed models. Graphs were generated using "ggplot2" package in R (Wickham 2016; version 3.3.3).

RESULTS

There was a statistically significant negative main effect of transitivity ($B = -0.05$, $P = 0.023$; Figure 1; Table 2), whereby yellow-bellied marmots residing in groups with more connected, transitive social structures gained proportionally less mass during the summer growing season. This result is contrary to our a priori hypothesis for how transitivity was predicted to work. The model's marginal part R^2 explained 69.9% of the variance whereas transitivity on its own explained near zero percent of the variation, suggesting that its impact on mass gain is very modest. There was also a statistically significant positive main effect of cut points ($B = -0.074$, $P = 0.002$; Figure 1; Table 2), suggesting as groups become more fragmentable, marmots experience higher mass gain rates. This result is also contrary to our *a priori* hypothesis. However, the effect size of the network measure was again very modest, with the marginal part R^2 for cut points explaining near zero percent of the variation. Additional results for the relationship between social group structure and individual mass gain are highly context dependent and are based on an individual's life history stage.

There were five statistically significant interactions between the social network measures and age in our models: density, reciprocity, degree assortativity, diameter, and cut points (Figure 1; Table 2). The density and age interaction ($B = -0.034$, $P = 0.023$) explained 56.0% of (marginal part R^2) variation and suggests yearlings residing in more dense, connected social groups gained proportionally less mass than adult marmots. This was consistent with our *a priori* hypothesis for density. The interaction between reciprocity and age ($B = -0.043$, $P = 0.004$) followed a similar pattern, explaining 56.3% (marginal part R^2) variation and was not consistent with our hypotheses for this network measures. This suggests yearlings in groups with higher rates of mutual interactions gained less mass than adults in these groups.

Yearlings residing in socially homogeneous groups, as measured via degree assortativity ($B = 0.033$, $P = 0.029$, marginal part $R^2 = 56.2\%$), gained more mass than adults in these homogeneous groups. This is partially consistent with our hypothesis which predicted a main effect, but not an age-specific effect. The interaction between diameter and age ($B = -0.029$, $P = 0.04$, marginal part $R^2 = 58.6\%$) suggests that adults gain proportionally more mass than yearlings as the distance between the two most distant nodes increases. The interaction between cut points and age ($B = 0.076$, $P < 0.001$) explained 57.2% of (marginal part R^2) variation and suggests that yearlings in less stable and more fragmentable groups gained more mass than adults. This result was not consistent with hypothesis for the cut points measure.

In addition to the two statistically significant main effects and five statistically significant interactions, the fixed effects of sex, age, and location were statistically significant in all seven models (Table 2). Each of these fixed effects explained an average of 2.0%, 56.1%, and 2.9% of (marginal part R^2) variation, respectively. Thus, these factors, notably age, explained a majority of model's variation. The random effects in our models explained an additional 14.6% of variation on average, meaning our models explained an average of 84.7% when incorporating both fixed and random effects (conditional part R^2).

DISCUSSION

Overall, we found a modest statistically significant negative relationship between proportional mass gain rate and the transitivity in marmot group social structure. We also found a modest statistically significant positive relationship between proportional mass gain rate and a network's cut points. These results complement each other, suggesting that as groups become more connected and less fragmentable, both adults and yearlings gain less mass. Since yellow-bellied marmots are a facultatively social species, and as more social and connected marmots on the individual level experience more costs than benefits (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018), these findings are not unexpected and contribute to our understanding of the consequences of marmot social behavior.

By residing in a more socially connected group, individuals may have to allocate time and energy towards social interactions instead of feeding. Individuals are more likely to be subjected to social interactions in more connected groups (Wasserman and Faust 1994). This negative relationship was contrary to our hypothesis which was informed by Wey et al. (2019), who showed that more affiliative social groups exhibit higher rates of transitivity. Despite transitivity occurring at higher rates in affiliative groups, our findings suggest transitivity is costly for mass gain. Although affiliative behavior may structure transitive relationships in social groups, ultimately this transitivity comes at a potential cost to winter survival. However, these costs may be potentially offset by benefits accrued over the summer, whereby individuals in more connected groups are better able to detect and avoid predators (Janson and Goldsmith 1995; Clutton-Brock et al. 1999).

In addition to the main effects, there were five statistically significant interactions between age and attributes of social structure: density, reciprocity, degree assortativity, diameter, and cut points. These interactions suggest that the specific nature of social structure's relationship with mass gain depends on an individual's life history stage.

As density increases, yearlings experience sharper declines in mass gain rate than adults. This coincides with previous work in this system showing adults, and especially adult females, tended to become less social as they aged (Wey and Blumstein 2010). This suggests adults are more buffered from the connectivity of their social group than yearlings, who are responsible for the majority of the social interactions that structure marmot groups. Additionally,

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

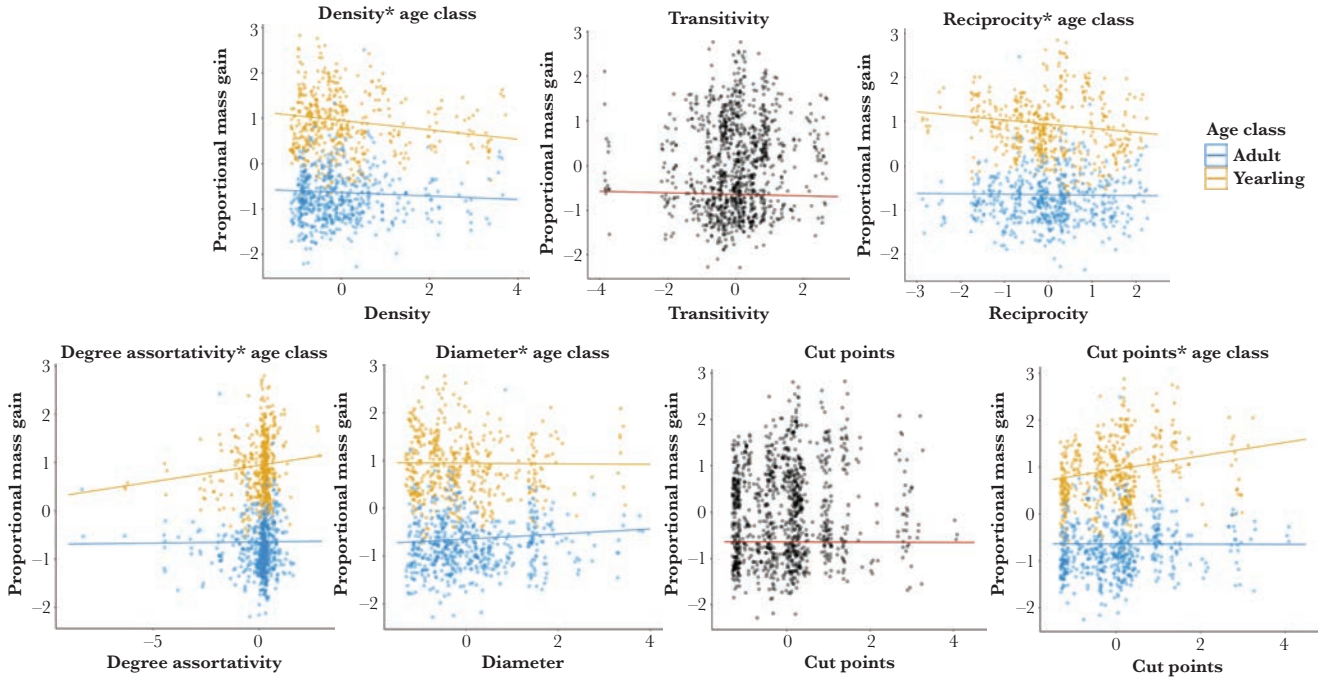


Figure 1

Relationship between attributes of social structure and mass gain. Transitivity and cut points are the statistically significant main effects. All others are statistically significant interactions between attributes of social structure and age. The predictor variable is standardized whereas the response variable was $\log_{10}$-transformed and standardized.

as the length between the two most distant noes increases, adults gain mass at a statistically significant higher rate than yearlings. Larger diameters can occur with decreased connectedness, thus complementing the finding for density. These results may be associated with marmots being facultatively social, in that they experience fitness consequences from connected social structures.

Perhaps surprisingly, yearlings in more reciprocal social groups experienced suppressed mass gain rates. Reciprocity, an important concept for the evolution of behaviors such as grooming (Silk et al. 1999), cooperation (van Doorn and Taborsky 2012), and dominance hierarchies (Solomon-Lane et al. 2015), is typically hypothesized to be beneficial in affiliative scenarios. Surprisingly, we found the opposite. This may be because reciprocity creates the potential for more interactions, and as seen with the results for density and transitivity, higher rates of interaction or connectivity is a detriment for marmots. However, yearlings residing in groups comprised of individuals with more homophilic social profiles to their own (degree assortativity) experience greater benefits for mass gain than adults. In general, higher social homophily in a group may lead to a reduction in social stressors as interactions are more predictable and reliable (Massen and Koski 2014). In our case, social homophily may be beneficial in terms of mass gain for yearlings because having similar social partners can reduce the energy tradeoff between maintaining and participating in social relationships and foraging behavior and antipredator vigilance.

Yearlings, more so than adults, also experienced a statistically significant positive relationship between mass gain and cut points – which reflects the stability of a group from fracturing into two separate groups. When residing in fragmentable groups, yearlings gained proportionally more mass. This is potentially similar to the finding for density, which suggested residing in more connected social groups was detrimental for yearling's mass gain rates. As groups become less connected, and in turn more easily fractured into separate groups, yearling marmots fair better. However, there was a statistically significant main effect of cut points, suggesting that residing in fragmentable groups is potentially beneficial for all marmots, though the effect sizes and overall trend were very modest. This is again supported by marmots being facultatively social and experiencing costs from being more connected on the individual level (Wey and Blumstein 2012; Fuong et al. 2015; Blumstein et al. 2018).

Our use of the "partR2" package to estimate marginal and conditional part R^2 values to identify the variance explained by each fixed effect and the random effects as a whole is not without its difficulties. "partR2" is a relatively new package, especially in the behavioral ecology and social network literatures. In our results, it appears that our part R^2 variances are additive (combinations of predictors explain about the sum of the variance explained by individual predictors). As we use Gaussian models, this additive nature of the variances is expected (Stoffel et al. 2021). An aspect worth discussion of using part R^2 values to calculate the variance explained is the difficulty in fully identifying the variance explained by the interaction between two fixed effects, and not just the two part R^2 values of the two fixed effects pooled together. Stoffel et al. (2021) explores this topic in more detail and proposes that while the part R^2 value for an interaction may seem simply additive, the variance actually explained by that interaction is more nuanced. Thus, although it may appear that one fixed effect contributes most, if not all, of the explained variance for an interaction, effect size of the interaction may actually be larger.

We acknowledge that a potential limitation of this study is our use of BLUPs, which can lead to anticonservative estimates of individual masses, and thus higher rates of Type 1 error (Hadfield et al. 2010; Houslay and Wilson 2017). However, our large dataset used to produce the BLUPs helps to mitigate this error (Dingemanse et al. 2019). Hadfield et al. (2010) and Houslay and Wilson (2017)

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

Table 2

Model estimates, standard error, *P* value, and marginal part R^2 for fixed effects. Values in bold represent statistical significance ($P < 0.05$). In addition to estimated part R^2 values for the models, estimated 95% confidence intervals based on 100 parametric bootstrap iterations are reported in paratheses. Data on the random effects can be found in Supplementary Table 2

		Intercept	Network Measure	Group Size	Sex	Age	Valley Location	n Mass Observations	Network Measure * Valley Location	Network Measure * Age	Network Measure * Sex
Density	Est. ± SE	0.032 ± 0.079	−0.049 ± 0.03	−0.046 ± 0.042	−0.102 ± 0.016	0.787 ± 0.015	−0.232 ± 0.026	−0.007 ± 0.015	0.017 ± 0.023	−0.034 ± 0.015	0.003 ± 0.015
	P value	0.692	0.105	0.282	**<0.001**	**<0.001**	**<0.001**	0.636	0.46	**0.023**	0.831
	Marginal part R^2	0.7 (0.642–0.74)	0 (0–0.047)	0 (0–0.047)	0.02 (0–0.07)	0.558 (0.51–0.596)	0.036 (0–0.086)	0 (0–0.051)	0.031 (0–0.081)	0.56 (0.513–0.599)	0.016 (0–0.066)
	Conditional part R^2	0.855 (0.831–0.878)	0.138 (0.069–0.208)	0.138 (0.07–0.209)	0.163 (0.097–0.232)	0.711 (0.683–0.742)	0.178 (0.113–0.246)	0.142 (0.074–0.212)	0.173 (0.107–0.241)	0.714 (0.686–0.744)	0.159 (0.092–0.228)
Transitivity	Est. ± SE	0.034 ± 0.079	−0.05 ± 0.022	−0.011 ± 0.033	−0.102 ± 0.016	0.789 ± 0.015	−0.231 ± 0.025	−0.003 ± 0.016	−0.001 ± 0.022	−0.025 ± 0.015	0.016 ± 0.015
	P value	0.676	**0.023**	0.742	**<0.001**	**<0.001**	**<0.001**	0.859	0.975	0.099	0.282
	Marginal part R^2	0.699 (0.651–0.743)	0 (0–0.051)	0 (0–0.054)	0.02 (0–0.074)	0.559 (0.518–0.605)	0.034 (0–0.087)	0 (0–0.055)	0.028 (0–0.082)	0.56 (0.519–0.606)	0.016 (0–0.07)
	Conditional part R^2	0.854 (0.833–0.878)	0.138 (0.073–0.216)	0.141 (0.076–0.219)	0.163 (0.1–0.239)	0.713 (0.685–0.747)	0.175 (0.113–0.25)	0.142 (0.077–0.22)	0.169 (0.106–0.245)	0.714 (0.686–0.747)	0.159 (0.096–0.236)
Reciprocity	Est. ± SE	0.032 ± 0.08	−0.047 ± 0.027	−0.015 ± 0.034	−0.102 ± 0.016	0.787 ± 0.015	−0.221 ± 0.026	−0.004 ± 0.015	0.008 ± 0.024	−0.043 ± 0.015	0.006 ± 0.015
	P value	0.699	0.092	0.653	**<0.001**	**<0.001**	**<0.001**	0.813	0.744	**0.004**	0.681
	Marginal part R^2	0.7 (0.652–−0.748)	0.003 (0–0.046)	0 (0–0.043)	0.02 (0–0.062)	0.562 (0.516–0.604)	0.036 (0–0.078)	0 (0–0.044)	0.037 (0–0.078)	0.563 (0.518–0.605)	0.023 (0–0.065)
	Conditional part R^2	0.857 (0.838–0.874)	0.147 (0.082–0.207)	0.143 (0.079–0.204)	0.165 (0.102–0.224)	0.718 (0.692–0.742)	0.18 (0.117–0.237)	0.144 (0.08–0.205)	0.18 (0.118–0.238)	0.719 (0.693–0.742)	0.168 (0.105–0.227)
Degree Assortativity	Est. ± SE	0.03 ± 0.077	0.016 ± 0.021	−0.01 ± 0.036	−0.104 ± 0.016	0.793 ± 0.015	−0.22 ± 0.027	−0.011 ± 0.015	−0.009 ± 0.019	0.031 ± 0.015	0.011 ± 0.014
	P value	0.703	0.438	0.779	**<0.001**	**<0.001**	**<0.001**	0.466	0.63	**0.039**	0.434
	Marginal part R^2	0.713 (0.658–0.767)	0 (0–0.051)	0 (0–0.051)	0.021 (0–0.071)	0.571 (0.523–0.617)	0.034 (0–0.084)	0 (0–0.052)	0.032 (0–0.082)	0.573 (0.525–0.619)	0.02 (0–0.071)
	Conditional part R^2	0.855 (0.834–0.875)	0.141 (0.065–0.207)	0.141 (0.065–0.207)	0.162 (0.089–0.227)	0.712 (0.686–0.737)	0.175 (0.103–0.239)	0.142 (0.066–0.208)	0.173 (0.101–0.237)	0.714 (0.688–0.738)	0.162 (0.088–0.227)
Diameter	Est. ± SE	0.03 ± 0.079	0.024 ± 0.031	0.019 ± 0.044	−0.104 ± 0.016	0.794 ± 0.015	−0.224 ± 0.027	−0.011 ± 0.015	−0.007 ± 0.025	−0.029 ± 0.014	−0.008 ± 0.014
	P value	0.703	0.44	0.66	**<0.001**	**<0.001**	**<0.001**	0.461	0.784	**0.04**	0.586
	Marginal part R^2	0.711 (0.655–0.756)	0 (0–0.058)	0.001 (0–0.058)	0.021 (0–0.077)	0.572 (0.524–0.614)	0.026 (0–0.082)	0 (0–0.058)	0.032 (0–0.087)	0.574 (0.526–0.616)	0.02 (0–0.077)
	Conditional part R^2	0.855 (0.839–0.877)	0.144 (0.076–0.216)	0.145 (0.077–0.216)	0.165 (0.098–0.235)	0.716 (0.691—0.747)	0.169 (0.104–0.239)	0.144 (0.077–0.216)	0.175 (0.11–0.245)	0.718 (0.693–0.749)	0.164 (0.098–0.235)

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

Table 2
Continued

		Intercept	Network Measure	Group Size	Sex	Age	Valley Location	n Mass Observations	Network Measure * Valley Location	Network Measure * Age	Network Measure * Sex
Cut Points	Est. ± SE	0.034 ± 0.074	0.074 ± 0.023	−0.006 ± 0.032	−0.108 ± 0.015	0.795 ± 0.015	−0.227 ± 0.025	−0.005 ± 0.015	0.004 ± 0.022	0.073 ± 0.014	0.001 ± 0.014
	P value	0.652	**0.002**	0.845	**<0.001**	**<0.001**	**<0.001**	0.756	0.847	**<0.001**	0.965
	Marginal part R^2	0.725 (0.654–0.777)	0.001 (0–0.045)	0 (0–0.044)	0.021 (0–0.065)	0.58 (0.524–0.626)	0.032 (0–0.076)	0 (0–0.044)	0.032 (0–0.076)	0.586 (0.53–0.633)	0.022 (0–0.066)
	Conditional part R^2	0.857 (0.837–0.877)	0.134 (0.072–0.218)	0.132 (0.07–0.217)	0.154 (0.093–0.237)	0.712 (0.686–0.745)	0.165 (0.105–0.247)	0.133 (0.071–0.218)	0.165 (0.105–0.247)	0.719 (0.693–0.751)	0.155 (0.095–0.238)
Centralization	Est. ± SE	0.026 ± 0.077	0.006 ± 0.021	0.004 ± 0.037	−0.103 ± 0.016	0.793 ± 0.015	−0.229 ± 0.027	−0.01 ± 0.015	0.022 ± 0.02	−0.03 ± 0.015	−0.001 ± 0.014
	P value	0.739	0.772	0.924	**<0.001**	**<0.001**	**<0.001**	0.51	0.263	0.052	0.954
	Marginal part R^2	0.713 (0.665–0.753)	0 (0–0.057)	0 (0–0.057)	0.02 (0–0.076)	0.572 (0.534–0.613)	0.034 (0–0.089)	0 (0–0.057)	0.034 (0–0.089)	0.574 (0.536–0.614)	0.02 (0–0.076)
	Conditional part R^2	0.855 (0.838–0.878)	0.142 (0.073–0.206)	0.142 (0.073–0.206)	0.162 (0.095–0.225)	0.714 (0.69–0.744)	0.176 (0.109–0.238)	0.142 (0.073–0.206)	0.176 (0.109–0.238)	0.716 (0.692–0.746)	0.163 (0.095–0.225)

proposed that to avoid anticonservative estimates the mean and mode of the posterior distribution of each BLUP could be used. We did not use this because the estimates from lme4 are equivalent. If Hadfield et al. (2010) and Houslay and Wilson (2017) are correct that the mean and mode are different from the lme4 estimates and would lead to more conservative estimates when the trait of interest is complex, it is less than straightforward to apply in our system. In our system mass gain is age and sex-specific with a nonlinear relationship with the date and is also specific to each year due to annual variation in environmental effects (Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger et al. 2020). Thus, modeling mass gain as a trait using the Hadfield et al. (2010) and Houslay and Wilson (2017) approach would be difficult to parametrize as a single model with age, sex, and year specific non-linear effects to get the estimation of individual year specific BLUPs with a posterior distribution. Therefore, we believe that our method and use of BLUPs in this study is reasonable.

In summary, we have discovered novel associations between the social structure of the group in which an individual resides and an important fitness consequence--mass gain rate. Although effect sizes for these attributes of group social structure were modest, using social network analysis and network-level measures proved to be a valuable tool to illuminate this social structure-fitness relationship. Although social structure did have a modest significant relationship, an individual's age, sex, and location explained significant variation in mass gain rate. This supports the findings from Heissenberger et al. (2020) that age and location are the primary drivers of mass gain. Additional studies are required to further identify the consequence of social structure in this system to better inform our understanding of the fitness consequences of sociality for facultatively social species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by the National Geographic Society; UCLA (Faculty Senate and the Division of Life Sciences); a Rocky Mountain Biological Laboratory and the 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 RMBL).

We thank the many previous marmoteers who have collected data throughout the years, Dana Williams, Ph.D. for assistance with social network code, Julien Martin, Ph.D. for managing the database and statistical advice, and Victoria Reynolds, Ph.D. for assistance in figure assembly. We also thank Alfredo Sánchez-Tójar, Ph.D., Rich McFarland, Ph.D., an anonymous reviewer, and the editors at *Behavioural Ecology* for their insightful comments that helped improve our manuscript. Data were collected under the UCLA Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and with permission from the Colorado Parks and Wildlife (TR917, renewed annually).

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 (2021)

Handling editor: Amanda Ridley

REFERENCES

Allainé D, Graziani L, Coulon J. 1998. Postweaning mass gain in juvenile alpine marmots *Marmota marmota*. Oecologia. 113(3):370–376.

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

Amir N, Whitehouse ME, Lubin Y. 2000. Food consumption rates and competition in a communally feeding social spider, *Stegodyphus dumicola* (Eresidae). J Arachnol. 28(2):195–200.
Armitage KB. 1962. Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). Anim Behav. 10(3–4):319–331.
Armitage KB. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu Rev Ecol Syst. 22(1):379–407.
Armitage KB. 1998. Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. J Mammal. 79:385–393.
Armitage KB. 2014. Marmot biology: sociality, individual fitness, and population dynamics. Cambridge (MA): Cambridge University Press.
Armitage KB, Blumstein DT, Woods BC. 2003. Energetics of hibernating yellow-bellied marmots (Marmota flaviventris). Comp Biochem Physiol A Mol Integr Physiol. 134(1):101–114.
Armitage KB, Downhower JF, Svendsen GE. 1976. Seasonal changes in weights of marmots. Am Midl Nat. 96(1):36–51. doi: 10.2307/2424566.
Armitage KB, Salsbury CM, Barthelmess EL, Gray RC, Kovach A. 1996. Population time budget for the yellow-bellied marmot. Ethol Ecol Evol. 8(1):67–95.
Armitage KB, Wolff JO, Sherman PW. 2007. Evolution of sociality in marmots: it begins with hibernation. Chicago (IL): University of Chicago Press. p. 356–367.
Atkinson SN, Ramsay MA. 1995. The effects of prolonged fasting of the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct Ecol. 9(4):559–567.
Bachman GC. 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Anim Behav. 46(2):233–244.
Bairlein F. 2002. How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. Naturwissenschaften. 89(1):1–10.
Bates D, Maechler M, Bolker B, Walker S. 2015. lme4: linear mixed-effects models using 'Eigen' and S4, R package version 1.1–10. Available from http://CRAN.R-project.org/package=lme4. Accessed 20 July 2020.
Becker RA, Chambers JM, Wilks AR. 1988. The new S language. Belmont (CA): Wadsworth & Brooks/Cole.
Blem CR. 1980. The energetics of migration. Animal migration, orientation, and navagation. Amsterdam (NL): Elesiver. pp. 175–224.
Blumstein DT, Keeley KN, Smith JE. 2016. Fitness and hormonal correlates of social and ecological stressors of female yellow-bellied marmots. Anim Behav. 112:1–11.
Blumstein DT, Ozgul A, Yovovitch V, Van Vuren DH, Armitage KB. 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. J Zool. 27:132–138.
Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc R Soc B Biol Sci. 276(1669):3007–3012.
Blumstein DT, Williams DM, Lim AN, Kroeger S, Martin JGA. 2018. Strong social relationships are associated with decreased longevity in a facultatively social mammal. Proc R Soc B Biol Sci. 285:20171934.
Blundell GM, Ben-David M, Bowyer RT. 2002. Sociality in river otters: cooperative foraging or reproductive strategies? Behav Ecol. 13(1):134–141.
Borgatti SP. 2006. Identifying sets of key players in a social network. Comput Math Org Theory. 12(1):21–34.
Broder A, Kumar R, Maghoul F, Raghavan P, Rajagopalan S, Stata R, Tomkins A, Wiener J. 2000. Graph structure in the web. Comput Netw. 33(1–6):309–320.
Burt RS. 1992. Structural holes: the social structure of competition. Cambridge (MA): Harvard University Press.
Burton NH, Rehfisch MM, Clark NA, Dodd SG. 2006. Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. J Appl Ecol. 43(3):464–473.
Cameron GN, Spencer SR. 1983. Field growth rates and dynamics of body mass for rodents on the Texas coastal prairie. J Mammal. 64(4):656–665.
Chapman CA, Valenta K. 2015. Costs and benefits of group living are neither simple nor linear. Proc Natl Acad Sci. 112(48):14751–14752.
Chastel O, Weimerskirch H, Jouventin P. 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. Auk. 112(4):964–972.
Clark CW, Dukas R. 1994. Balancing foraging and antipredator demands: an advantage of sociality. Am Nat. 144(3):542–548.
Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll ADC, Kansky R, Chadwick P, Manser M, Skinner JD, Brotherton PNM. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J Anim Ecol. 68(4):672–683.
Côté IM, Poulinb R. 1995. Parasitism and group size in social animals: a meta-analysis. Behav Ecol. 6(2):159–165.
Crino OL, Buchanan KL, Trompf L, Mainwaring MC, Griffith SC. 2017. Stress reactivity, condition, and foraging behavior in zebra finches: effects on boldness, exploration, and sociality. Gen Comp Endocrinol. 244:101–107.
Csardi G, Nepusz T. 2006. The igraph software package for complex network research. Int J Commun Syst. 1695(5):1–9.
Currarini S, Matheson J, Vega-Redondo F. 2016. A simple model of homophily in social networks. Eur Econ Rev. 90:18–39.
Dark J. 2005. Annual lipid cycles in hibernators: integration of physiology and behavior. Annu Rev Nutr. 25:469–497.
Davis GH, Crofoot MC, Farine DR. 2018. Estimating the robustness and uncertainty of animal social networks using different observational methods. Anim Behav. 141:29–44.
Dindo M, Whiten A, de Waal FB. 2009. Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). Am J Primatol. 71(5):419–426.
Dingemanse NJ, Moiron M, Araya-Ajoy YG, Mouchet A, Abbey-Lee RN. 2019. Individual variation in age-dependent reproduction: fast explorers live fast but senesce young? J Anim Ecol. 89(2):601–613.
Dunn EH. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson J Ornithol. 114(3):368–379.
Ezenwa VO, Ghai RR, McKay AF, Williams AE. 2016. Group living and pathogen infection revisited. Curr Opin Behav Sci. 12:66–72.
Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol. 84(5):1144–1163.
Faust K. 2010. A puzzle concerning triads in social networks: graph constraints and the triad census. Soc Netw. 32:221–233.
Franke GR. 2010. Multicollinearity. Wiley international encyclopedia of marketing. Chicago: Wiley.
Frase BA, Hoffmann RS. 1980. *Marmota flaviventris*. Mamm Species. (135):1–8. doi: 10.2307/3503965.
Freeman LC. 1979. Centrality in social networks conceptual clarification. Soc Netw. 1:215–239.
French AR. 1985. Allometries of the durations of torpid and euthermic intervals during mammalian hibernation: a test of the theory of metabolic control of the timing of changes in body temperature. J Comp Physiol B. 156(1):13–19.
Fuong H, Maldonado-Chaparro A, Blumstein DT. 2015. Are social attributes associated with alarm calling propensity? Behav Ecol. 26(2):587–592.
Galloway AT, Addessi E, Fragaszy DM, Visalberghi E. 2005. Social facilitation of eating familiar food in tufted capuchins (*Cebus apella*): does it involve behavioral coordination? Int J Primatol. 26:181–189.
Green AJ. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology. 82(5):1473–1483.
Grund TU. 2012. Network structure and team performance: the case of English Premier League soccer teams. Soc Netw. 34:682–690.
Hadfield JD, Wilson AJ, Garant D, Sheldon BC, Kruuk LE. 2010. The misuse of BLUP in ecology and evolution. Am Nat. 175(1):116–125.
Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31(2):295–311.
Haramis GM, Nichols JD, Pollock KH, Hines JE. 1986. The relationship between body mass and survival of wintering canvasbacks. Auk. 103(3):506–514.
Harris DB, Macdonald DW. 2007. Interference competition between introduced black rats and endemic Galápagos rice rats. Ecology. 88(9):2330–2344.
Hass CC, Valenzuela D. 2002. Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). Behav Ecol Sociobiol. 51(6):570–578.
Hebblewhite M, Pletscher DH. 2002. Effects of elk group size on predation by wolves. Can J Zool. 80(5):800–809.
Heissenberger S, de Pinho GM, Martin JG, Blumstein DT. 2020. Age and location influence the costs of compensatory and accelerated growth in a hibernating mammal. Behav Ecol. 31(3):826–833.
Houslay TM, Wilson AJ. 2017. Avoiding the misuse of BLUP in behavioural ecology. Behav Ecol. 28(4):948–952.
Hughes WO, Eilenberg J, Boomsma JJ. 2002. Trade-offs in group living: transmission and disease resistance in leaf-cutting ants. Proc R Soc Lond Ser B Biol Sci. 269(1502):1811–1819.

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

Jakob EM. 1991. Costs and benefits of group living for pholcid spiderlings: losing food, saving silk. Anim Behav. 41(4):711–722.
Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6(3):326–336.
Kang SM. 2007. Equicentrality and network centralization: a micro–macro linkage. Soc Netw. 29(4):585–601.
Kankanhalli A, Tan B, Wei K. 2005. Contributing knowledge to electronic knowledge repositories: an empirical investigation. Manag. Inf. Syst. Q. 29(1):113–143.
Kappeler PM. 2019. A framework for studying social complexity. Behav Ecol Sociobiol. 73(1):13.
Kiell DJ, Millar JS. 1978. Growth of juvenile arctic ground squirrels (*Spermophilus parryii*) at McConnell River, NWT. Can J Zool. 56(7):1475–1478.
Klaassen M, Biebach H. 1994. Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. J Comp Physiol B. 164(5):362–371.
Krause J, Ruxton GD, Ruxton GD, Ruxton IG. 2002. Living in groups. Oxford (UK): Oxford University Press.
Kroeger SB, Blumstein DT, Armitage KB, Reid JM, Martin JG. 2018. Age, state, environment, and season dependence of senescence in body mass. Ecol Evol. 8(4):2050–2061.
Lancaster JR, Wilson P, Espinoza RE. 2006. Physiological benefits as precursors of sociality: why banded geckos band. Anim Behav. 72(1):199–207.
Lenihan C, Vuren DV. 1996. Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). Can J Zool. 74(2):297–302.
Lovegrove BG, Wissel C. 1988. Sociality in molerats. Oecologia. 74(4):600–606.
Lüdecke D, Makowski D, Waggoner P, Patil I. 2020. Performance: assessment of regression models performance. R package version 0.4.7. https://CRAN.R-project.org/package=performance. Accessed 13 August 2020.
Lyman CP, Chatfield PO. 1955. Physiology of hibernation in mammals. Physiol Rev. 35(2):403–425.
Majolo B, de Bortoli Vizioli A, Schino G. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim Behav. 76(4):1235–1247.
Maldonado-Chaparro AA, Hubbard L, Blumstein DT. 2015a. Group size affects social relationships in yellow-bellied marmots (*Marmota flaviventris*). Behav Ecol. 26:909–915.
Maldonado-Chaparro AA, Martin JG, Armitage KB, Oli MK, Blumstein DT. 2015b. Environmentally induced phenotypic variation in wild yellow-bellied marmots. J Mammal. 96(2):269–278.
Maldonado-Chaparro AA, Read DW, Blumstein DT. 2017. Can individual variation in phenotypic plasticity enhance population viability? Ecol Modell. 352:19–30.
Manlove KR, Cassirer EF, Cross PC, Plowright RK, Hudson PJ. 2014. Costs and benefits of group living with disease: a case study of pneumonia in bighorn lambs (Ovis canadensis). Proc R Soc B Biol Sci. 281(1797):20142331.
Markham AC, Gesquiere LR. 2017. Costs and benefits of group living in primates: an energetic perspective. Philos Trans R Soc B Biol Sci. 372(1727):20160239.
Martin JGA, Pelletier F. 2011. Measuring growth patterns in the field: effects of sampling regime and methods on standardized estimates. Can J Zool. 89:529–537.
Masman D, Klaassen M. 1987. Energy expenditure during free flight in trained and free-living kestrels (*Falco tinnunculus*). Auk. 104:603–616.
Massen JJ, Koski SE. 2014. Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. Evol Hum Behav. 35(1):1–8.
McMahon CR, Burton HR, Bester MN. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. Antarct Sci. 12(2):149–153.
McPherson M, Smith-Lovin L, Cook JM. 2001. Birds of a feather: homophily in social networks. Annu Rev Sociol. 27(1):415–444.
Metcalfe NB, Furness RW. 1984. Changing priorities: the effect of premigratory fattening on the trade-off between foraging and vigilance. Behav Ecol Sociobiol. 15(3):203–206.
Millesi E, Strijkstra AM, Hoffmann IE, Dittami JP, Daan S. 1999. Sex and age differences in mass, morphology, and annual cycle in European ground squirrels, *Spermophilus citellus*. J Mammal. 80(1):218–231.
Milner JM, Stien A, Irvine RJ, Albon SD, Langvatn R, Ropstad E. 2003. Body condition in Svalbard reindeer and the use of blood parameters as indicators of condition and fitness. Can J Zool. 81(9):1566–1578.
Milo R, Shen-Orr S, Itzkovitz S, Kashtan N, Chklovskii D, Alon U. 2002. Network motifs: simple building blocks of complex networks. Science. 298:824–827.
Molvar EM, Bowyer RT. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. J Mammal. 75(3):621–630.
Monclús R, Pang B, Blumstein DT. 2014. Yellow-bellied marmots do not compensate for a late start: the role of maternal allocation in shaping life-history trajectories. Evol Ecol. 28:721–733.
Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol. 4(2):133–142.
Pennycuick CJ. 1975. Mechanics of flight. In: Farner DS and King JR, editors. Avian biology, vol. 5. Cambridge (MA): Academic Press. p. 1–75.
Pérez-Tris J, Díaz JA, Telleŕia JL. 2004. Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape? Anim Behav. 67(3):511–521.
Philson CP, Todorov SM, Blumstein DT. 2021. Marmot mass gain rates relate to their group's social structure. Behav Ecol. doi: 10.5068/D1X38H
Podlaszczuk P, Kamiński M, Włodarczyk R, Kaczmarek K, Janiszewski T, Minias P. 2016. Plumage quality mediates a life-history trade-off in a migratory bird. Front Zool.13(1):47.
Pollard KA, Blumstein DT. 2008. Time allocation and the evolution of group size. Anim Behav. 76:1683–1699.
R Development Core Team. 2020. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.
Ratcliffe L, Mennill DJ, Schubert KA. 2007. Social dominance and fitness in black-capped chickadees. Ecology and behavior of chickadees and titmice: an integrated approach. Oxford (UK): Oxford University Press.
Rauter CM, Moore AJ. 2002. Evolutionary importance of parental care performance, food resources, and direct and indirect genetic effects in a burying beetle. J Evol Biol. 15(3):407–417.
Rubenstein DI. 1978. On predation, competition, and the advantages of group living. In: Bateson P, editor. Social behavior. Boston (MA): Springer. p. 205–231.
Safi K, Kerth G. 2007. Comparative analyses suggest that information transfer promoted sociality in male bats in the temperate zone. Am Nat. 170(3):465–472.
Sánchez-Tójar A, Schroeder J, Farine DF. 2018. A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. J Anim Ecol. 87:594–608.
Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol. 1(2):103–113.
Schulte-Hostedde AI, Millar JS, Hickling GJ. 2001. Evaluating body condition in small mammals. Can J Zool. 79(6):1021–1029.
Shrestha N. 2020. Detecting multicollinearity in regression analysis. Am J Appl Math Stat. 8(2):39–42.
Silk MJ, Jackson AL, Croft DP, Colhoun K, Bearhop S. 2015. The consequences of unidentifiable individuals for the analysis of an animal social network. Anim Behav. 104:1–11.
Silk JB, Seyfarth RM, Cheney DL. 1999. The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. Behaviour. 136:679–703.
Solomon NG, Crist TO. 2008. Estimates of reproductive success for group-living prairie voles, *Microtus ochrogaster*, in high-density populations. Anim Behav. 76(3):881–892.
Solomon-Lane TK, Pradhan DS, Willis MC, Grober MS. 2015. Agonistic reciprocity is associated with reduced male reproductive success within haremic social networks. Proc R Soc B Biol Sci. 282:20150914.
Squartini T, Picciolo F, Ruzzenenti F, Garlaschelli D. 2013. Reciprocity of weighted networks. Sci Rep. 3:2729.
Stevenson RD, Woods Jr. WA. 2006. Condition indices for conservation: new uses for evolving tools. Integr Comp Biol. 46(6):1169–1190.
Stoffel MA, Nakagawa S, Schielzeth H. 2021. partR2: Partitioning R^2 in generalized linear mixed models. PeerJ. 9:e11414.
Testa JW, Adams GP. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). J Mammal. 79(4):1345–1354.
van Doorn GS, Taborsky M. 2012. The evolution of generalized reciprocity on social interaction networks. Evolution. 66:651–664.

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022

Van Vuren DH, Armitage KB. 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Can J Zool. 69:1755–1758.
Wasserman S, Faust K. 1994. Social network analysis: methods and applications, vol. 8. Cambridge (MA): Cambridge University Press.
Watts DJ, Strogatz SH. 1998. Collective dynamics of 'small-world' networks. Nature. 393(6684):440–442.
Weidt A, Hofmann SE, König B. 2008. Not only mate choice matters: fitness consequences of social partner choice in female house mice. Anim Behav. 75(3):801–808.
Wey TW, Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. Anim Behav. 79(6):1343–1352.
Wey TW, Blumstein DT. 2012. Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. Behav Ecol Sociobiol. 66:1075–1085.
Wey TW, Jordán F, Blumstein DT. 2019. Transitivity and structural balance in marmot social networks. Behav Ecol Sociobiol. 73:88.
Wickham H. 2016. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.
Willis CK. 2017. Trade-offs influencing the physiological ecology of hibernation in temperate-zone bats. Integr Comp Biol. 57(6):1214–1224.
Yang WJ, Maldonado-Chaparro A, Blumstein DT. 2017. A cost of being amicable in a hibernating mammal. Behav Ecol. 28(1):11–19.

Downloaded from https://academic.oup.com/beheco/article/33/1/115/6406609 by University of California, Los Angeles user on 21 February 2022