Behavioral Ecology

The official journal of the ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2015), 26(3), 909–915. doi:10.1093/beheco/arv034

Original Article

Group size affects social relationships in yellow-bellied marmots (*Marmota flaviventris*)

Adriana A. Maldonado-Chaparro,[a] Lilah Hubbard,[a] and Daniel T. Blumstein[a,b]
[a]Department of Ecology and Evolutionary Biology, University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA and [b]The Rocky Mountain Biological Laboratory, Box 519, Crested Butte, CO 81224, USA

Received 31 July 2014; revised 21 February 2015; accepted 26 February 2015; Advance Access publication 15 April 2015.

Demographic variation, such as changes in population size, affects group-living conditions and thus creates new opportunities for individuals to interact socially. To understand how this variation in the social environment affects social structure, we used social network analysis to explore affiliative behaviors of nonpup (i.e., 1 year or older), female, yellow-bellied marmots (*Marmota flaviventris*). We examined 4 social attributes (outdegree, indegree, closeness centrality, and betweenness centrality) to measure social plasticity in response to group size variation. We found that, in response to increases in group size, individuals established fewer social connections than possible, which suggests that marmots experience constraints on sociality. Similarly, closeness and betweenness centrality decreased as group size increased, suggesting that females are expected to lose influence over other members of the group as group size increases, and there are substantial constraints on marmots transmitting information to others in large groups. Our results also suggest that group-level responses, such as behavioral plasticity, can be explained by individual-level mechanisms that evaluate the costs and benefits of sociality. Interestingly, the mechanistic basis of these group-level responses may, at times, follow patterns expected by chance. We propose that further research is necessary to uncover the mechanisms underlying the individual-level behavioral response. Like group size effects studied in other domains, formally considering group size effects on social structure may shed novel light on the constraints on sociality.

Key words: **centrality, degree, group size effects, social networks, yellow-bellied marmots.**

INTRODUCTION

Ecological variation creates demographic opportunities that allow individuals to aggregate and form social groups (Blumstein 2013). Ecological factors (e.g., food availability and climate) can affect population characteristics, such as survival and reproduction, and thus drive variation in social groups and social systems (Butler 1980; Crockett and Eisenberg 1987). Such population level effects may increase or decrease with changes in group size and may create new opportunities for individuals to interact if they are not otherwise constrained. Therefore, in group-living animals, sociodemographic variation may affect social structure (Griffiths and Magurran 1997; Blumstein 2013; Schradin 2013). We view the social system as the group of conspecifics that consistently interact with each other and do so more often with each other than with individuals of other groups (Kappeler and van Schaik 2002), the social structure as the pattern of social interactions and the resulting relationships among individuals in the social system (Hinde 1976; Kappeler et al. 2013), and social organization as the size, sexual composition, and cohesion of a social system (Kappeler and van Schaik 2002; Kappeler et al. 2013).

Sociodemographic variation may differently affect a population's or a species' social organization, mating system, and social structure. Previous studies have shown that increases in group size can lead to the formation of complex societies that are characterized by a higher degree of morphological dimorphism and social roles (Bourke 1999), can increase male mating success (Alexander 1974; Hovi et al. 1994), and can also be associated with reduced offspring survival and declining birth rates after a certain group size is reached (van Noordwijk and van Schaik 1999). Primate studies that focused on the relationship between group size and social structure found that grooming increases with group size, but further increases in group size leads to constraints: individuals have insufficient time to allocate to maintaining their social relationships (Lehmann et al. 2007; Pollard and Blumstein 2008). Such findings suggest that individuals can modify their behavior and consequently alter the social relationships that emerge with changes in group size. Thus, we aimed to explore how differences in group size are associated with variation in individuals' social attributes that affect group structure. By doing so, we sought to identify the

---

Address correspondence to D.T. Blumstein. E-mail: marmots@ucla.edu.

mechanisms that permit females to behaviorally respond to changes in their social environment.

The relationships that individuals can establish with other members of the group may vary in the face of varying ecological and social conditions. Such changes in an individual's behavior as a function of the conditions they experience are defined as phenotypic plasticity (Bradshaw 1965; Stearns 1989; Pigliucci 2001). Plasticity of behavioral traits is known as behavioral plasticity (West-Eberhard 1989; Dingemanse and Wolf 2013). Thus, social plasticity can be defined as the ability of an individual to modify its social behavior (social interactions and relationships) in response to the social environment that it experiences (i.e., when found in different sized groups). We suggest that individuals modify their social behavior as a function of changes in their social environment through social plasticity. By documenting the nature of these plastic responses, we can understand how these behavioral changes alter the overall social structure of the social system and identify potential constraints on sociality.

Here, we used a population of yellow-bellied marmots (*Marmota flaviventris*; herein marmots), a diurnal and facultatively social rodent, as a study system to investigate variation in social structure in response to changes in the social environment. The marmot population around the Rocky Mountain Biological Laboratory (RMBL) offers a great opportunity to address this question, because females live in matrilines (i.e., kin groups), and the population size has dramatically increased over the past decade. This increase combined with a major population crash in 2011, probably as a result of warming spring temperatures and consequently an increase in food availability during the marmots' active season (Ozgul et al. 2010), has resulted in substantial variation in group size. Additionally, it has been suggested that marmots may increase affiliative behavior as group size increases to maintain social cohesion (i.e., the degree to which members of a group are connected to each other, Maldonado-Chaparro et al. 2015). Thus, in this study, we will concentrate on affiliative interactions because they are often important for both group social cohesion and individual fitness (Silk 2007b; Silk et al. 2009; Wey and Blumstein 2010, 2012) and because these interactions also play an important role for dispersal decisions (Blumstein et al. 2009).

We used social network analyses, which allowed us to statistically analyze the structure and components of networks that involve multiple types of interactions (Krause et al. 2009) and to study direct as well as indirect relationships (Wasserman and Faust 1994; Croft et al. 2008; Wey et al. 2008). We focused on 4 social network attributes that describe an individual's direct interactions and ability to influence other members of the group and allow us to quantify variation in an individual's behavioral response: outdegree, indegree, closeness centrality, and betweenness centrality. Outdegree quantifies the number of other individuals with whom an individual initiates interactions (Wasserman and Faust 1994), whereas indegree specifies the number of other individuals that direct interactions toward the subject (Wasserman and Faust 1994). Closeness centrality quantifies connectedness of an individual in terms of its direct and indirect interactions with every member of the group (i.e., measures an individual's influence), and betweenness centrality indicates the ability of a member to control paths of information (or disease) between members in a group. We chose these measures because they permitted us understand group structure (Freeman 1979) and to characterize how extensively individuals are involved in relationships with other individuals in the network. This permitted us to capture the propensity of an individual to develop social relationships as well as to quantify changes in the social dynamics of female marmots that may drive biological processes such as information or disease transmission.

We assumed that 1) changes in the social context offer new opportunities to interact with potential members of the group, 2) such additional social interactions lead to new relationships that may affect an individual's social network, and 3) individuals are able to optimize the assessment of alternative behavioral trade-offs. Given these assumptions, we hypothesized that females will adjust their affiliative social behavior in response to variation in group size to balance the cost–benefit trade-offs associated with social living. However, because individuals must also distribute their time and energy between social interactions and other activities, including foraging, resting, and traveling around their home ranges, the time available for interacting may act to constrain sociality (Dunbar 1992b; Pollard and Blumstein 2008; Blumstein 2013). Therefore, we also predicted that, as group size increases, individuals will increase the number of social partners until the cost of group living (i.e., increased competition over access to resources and mating opportunities, increased risk of disease, and increased predation risk) will exceed the benefit (i.e., protection from predators, increased foraging success, and reduced infanticide probability) and animals will be unable to engage in additional social relationships. Also, assuming that not all individuals in the group choose to increase the number of social partners (i.e., increase the number of direct connections), we expected animals to be less closely connected to other individuals in the group (i.e., lower closeness centrality) and to have less control over information flow (i.e., lower betweenness centrality).

METHODS

Monitoring social behavior and demography in yellow-bellied marmots

Since 1962, marmots in and around the RMBL have been regularly livetrapped and observed during the active season (between mid-April and early September). Using baited live traps, we trapped 100% of the individuals in our population annually. Individuals were given numbered ear tags the first time they were captured and were marked with fur dye for identification from afar (Blumstein et al. 2009). Additionally, we weighed (using a digital scale) and sexed each individual. Individuals were classified into 3 age categories: pups (<1 year), yearlings (1 year old), and adults (≥2 years old).

For these analyses, behavioral observations were conducted on an average of 53 females per year over a period of 12 years. We observed marmots from mid-April to early September, during hours of peak activity (from 7:00 to 10:00 h in the morning and 16:00 to 19:00 h in the afternoon; Blumstein et al. 2009). Observers sat quietly and observed marmots from about 20 to 150 m away (Blumstein et al. 2009) with binoculars and 15–45× spotting scopes. We recorded all observed social interactions (details in Wey and Blumstein 2010). For each individual interaction, we recorded the type (i.e., affiliative or agonistic), the initiator and recipient, the location, and the time of interaction. The number of hours of observation per year over the study period (2002–2013) averaged 874 h but varied from 302 to 1270 h (Supplementary Table S1).

Quantifying the social environment

The social context of yellow-bellied marmots can be hierarchically described. Marmots physically live in colony sites, a geographic area that may contain one or more social groups that are found in patches of suitable habitat. Social groups are a subset of 2 or more individuals that live in close proximity in space and time and thus are more associated among themselves than with other individuals in the colony site. Not all individuals in a social group are observed to interact above ground and thus animals in a social group may or may not interact to form social networks. Thus, group size may differ from social network size, which we defined as the set of individuals within a social group that were seen to behaviorally interact with other members of the group during the study period. A social network can be defined based on observations of affiliative interactions, agonistic interactions, or both.

We focused on individuals found in 4 geographically distinct areas (colony sites): Bench-River, Gothic Town, Marmot Meadow, and Picnic that are patchily distributed between 2700 and 3100 m.a.s.l. Our Marmot Meadow and Picnic sites are located in higher elevations (i.e., up valley) than our other 2 sites (i.e., down valley). Within each colony site, we identified social groups based on the marmot's space-use overlap (Smith JE, Strelioff CC, Blumstein DT, unpublished data). To do this, we focused on nonpup (i.e., 1 year or older) female and male marmots seen or trapped at least 5 times in a year. Then we used Socprog (Whitehead 2009) to calculate the simple ratio index (SRI, Cairns and Schwager 1987) from live-trapping and observation data for each pair of marmots. We then used the estimated SRI to identify the number and identity of the individuals that belonged to a particular social group (i.e., module) using the random walk algorithm on Map Equation (Rosvall and Bergstrom 2008; Rosvall et al. 2009). For the purpose of this study, we defined the social environment as the female group size (the number of nonpup females present in a social group) because we were interested in female sociality. Therefore, after identifying the members of each social group, we removed all males from the social group analysis to obtain the female group sizes. Between 2002 and 2013, we identified 86 social groups composed of 2 or more nonpup females. Nonpup female group sizes varied from 2 to 18 individuals for the years under study (Supplementary Table S2).

Quantifying individual social attributes

We focused on affiliative interactions (i.e., sit in body contact, sit in proximity, grooming, and social play) recorded during the entire active season to construct the affiliative social matrix and the corresponding social network for each social group in each colony site for each year from 2002 to 2013 (Figure 1). Social networks consisted of nodes (female marmots ≥1 year old) connected by directed edges (i.e., observed affiliative interactions between individuals). We calculated the 4 social attributes for each nonpup female individual in each social network (i.e., the connected components of the social group). Outdegree was computed as the number of connections initiated by an individual (Wasserman and Faust 1994). Indegree was the number of connections received by an individual (Wasserman and Faust 1994). Closeness centrality was calculated by taking the reciprocal of the sum of the shortest paths between the focal and other individuals (or the sum of the reciprocals) (Wasserman and Faust 1994; Wey et al. 2008; Wey and Blumstein 2012). Betweenness centrality was the proportion of shortest path lengths between pairs of other group members in which the focal individual was a point on the path (Wasserman and Faust 1994; Wey et al. 2008; Wey and Blumstein 2012). Outdegree and indegree were calculated using directed, unweighted networks, whereas closeness and betweenness centralities were calculated using undirected, unweighted networks.

All measurements were normalized to facilitate comparison across networks of different sizes; thus, all of our measurements ranged from 0 to 1. Indegree and outdegree were each divided by $n - 1$ (the maximum number of possible connections), where n was the total number of nodes in the network. For closeness, we multiplied the raw closeness by $n - 1$, where n was the number of nodes in the graph, whereas for betweenness, we used $2 \times B/(n \times n - 3 \times$

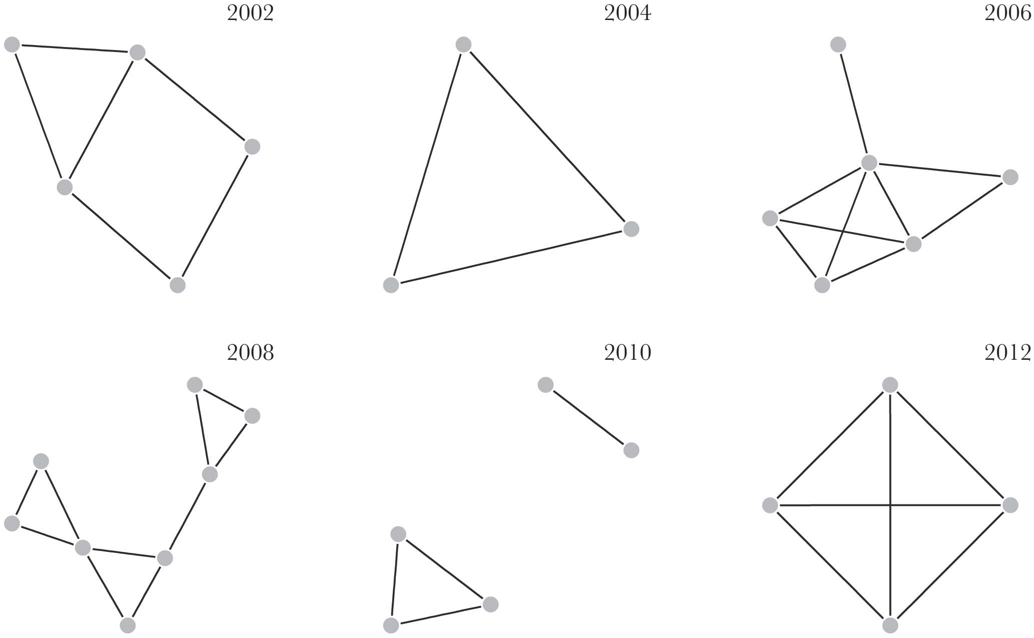

Figure 1
Examples of female (nonpup) yellow-bellied marmot (*Marmota flaviventris*) social networks in Marmot Meadow observed over different years. These networks differ in size and structure. Gray nodes: yearling and adult females; solid lines: undirected affiliative interactions.

$n + 2$), where B is the raw betweenness and n is the number of nodes in the graph (Freeman 1979). The unit of analysis was an individual studied in a given year. All our calculations were conducted in the iGraph package v. 0.7.1 (Csardi and Nepusz 2006) in R software v. 3.1.1 (R Core Team 2014).

Statistical analysis

To explore the potential relationship between group size and social structure, we performed a series of regression analyses that allowed us to identify group size effects. We used a reaction norm approach (Pigliucci 2001) to isolate the effect of group size on standardized network parameters. A simple linear reaction norm graph (i.e., straight line) contains 2 main characteristics: slope and elevation (Pigliucci 2001); however, more complex relations can be explained through nonlinear reaction norms (Koons et al. 2009). The slope quantifies the population's phenotypic plasticity, measured as the change in phenotypic expression with respect to environmental variation (Pigliucci 2001), and the elevation quantifies the average phenotypic response (Pigliucci 2001; Nussey et al. 2007). This approach allowed us to ask if social plasticity was a mechanism that explained variation in an individual's social attributes.

To describe the behavioral response pattern for each of our dependent variables, outdegree, indegree, closeness centrality, and betweenness centrality, we fitted a set of candidate mixed effect models that included linear and nonlinear relationships and performed a model selection analysis (Table 1). In each model, the dependent variable was modeled as a function of the year-specific social environment (i.e., female group size). We also included age category as a factor to control for known behavioral differences between yearlings and adults (Wey and Blumstein 2010; Maldonado-Chaparro et al. 2015). Additionally, and to account for repeated measures on individuals, we included female identity and year as random effects. The error structure of the models varied for each of the dependent variables. Outdegree and indegree were based on proportion data and therefore we fitted a binomial model (logit link) ($N_{\text{outdegree}} = 384$; $N_{\text{indegree}} = 384$). Closeness and betweenness centrality were arcsine square-root transformed and we fitted a Gaussian model (identity link) ($N_{\text{closeness}} = 395$). Betweenness centrality contained 80% of zeros. Thus, we focused only on the subset of our data where betweenness was greater than 0 ($N = 143$). We identified the best model supported by the data by using the Akaike information criterion corrected for small samples. For Gaussian models, we evaluated the significance of fixed effects using the Satterthwaite's approximation for degrees of freedom in the lmerTest package (Kuznetsova et al. 2014). All of our models were analyzed using the lme4 package (Bates et al. 2013) and the gamm4 package (Wood and Scheipl 2013) in R software (R Core Team 2014).

Finally, we assessed if the observed pattern in each of our social attributes differed from the pattern expected from social attributes estimated for random networks. To do this, for each of our observed social networks, we generated an equivalent Erdös–Rényi (E–R) random graph using the same number of n nodes. The probability (P) in E–R graphs can vary between 0 and 1, where 0 represents an empty graph and 1 represents a complete graph. Thus, we defined P as 0.5 to allow for the maximum uncertainty of a random graph (Takahashi et al. 2012). Then, we calculated the node-based indegree, outdegree, betweenness, and closeness in all of our E–R networks. We used the values obtained through the equivalent E–R graphs to create a data set that contained values expected by chance. We then used these random values as the response variable and fitted the best models that were selected for the observed values of outdegree, indegree, closeness, and betweenness. Finally, we built the 95% confidence intervals of the regression lines for the observed and the random data sets and determined if the confidence intervals overlapped. If they overlapped, the observed group size effect was expected by chance.

Table 1

Set of candidate models fitted for each of the 4 network measures (outdegree, indegree, closeness centrality, and betweenness centrality) calculated for members of the female social networks in yellow-bellied marmot (*Marmota flaviventris*)

Model	df	AIC_c
Outdegree		
Age category	5	511.80
Group size + age category	6	429.36
Group size + group size^2 + age category	**7**	**418.22**
s(Group size)	7	431.44
Indegree		
Age category	5	507.41
Group size + age category	6	395.65
Group size + group size^2 + age category	**7**	**390.01**
s(Group size)	7	397.71
Closeness centrality		
Age category	5	383.19
Group size + age category	**6**	194.81
Group size$_1$ + group size$_2$ + age category	**7**	**145.28**
s(Group size)	7	415.39
Betweenness centrality		
Age category	5	105.69
Group size + age category	6	89.32
Group size$_1$ + group size$_2$ + age category	**7**	**51.53**
s(Group size)	7	61.71

The model in bold represents the selected model based on the Akaike information criteria (AIC_c). Superscript 2 indicates squared group size and subscripts 1 and 2 indicate the slope for group size below and above the estimated breakpoint, respectively. s indicates the smooth function. df, degrees of freedom.

RESULTS

We constructed 86 nonpup female social networks based on observed affiliative interactions (some of the individuals in smaller spatially defined groups were not observed to interact). The observed networks had an average of 4.5 (±SD = 3.0) female marmots. As expected, our measures were somewhat correlated (i.e., indegree vs. outdegree, see Supplementary Figure S1), but we analyzed them independently because each one may reflect a different social process.

Our regression analyses revealed that group size was always significantly associated with an individual's social attributes, whereas age category was only sometimes significantly associated with an individual's social attributes. More precisely, outdegree and indegree declined nonlinearly with group size. For each additional member of the group, the probability that a female added an additional social partner initially decreased at an average of −0.339 (standard error [SE] = 0.04; $P < 0.001$) and then, for groups larger than 10, increased at an average of 0.026 (SE = 0.007; $P < 0.001$) social partners per additional individual (Figure 2a). Yearlings did not significantly differ from adults in their average response (0.432; SE = 0.251; $P = 0.086$). Our outdegree model explained 30.75% of the variance.

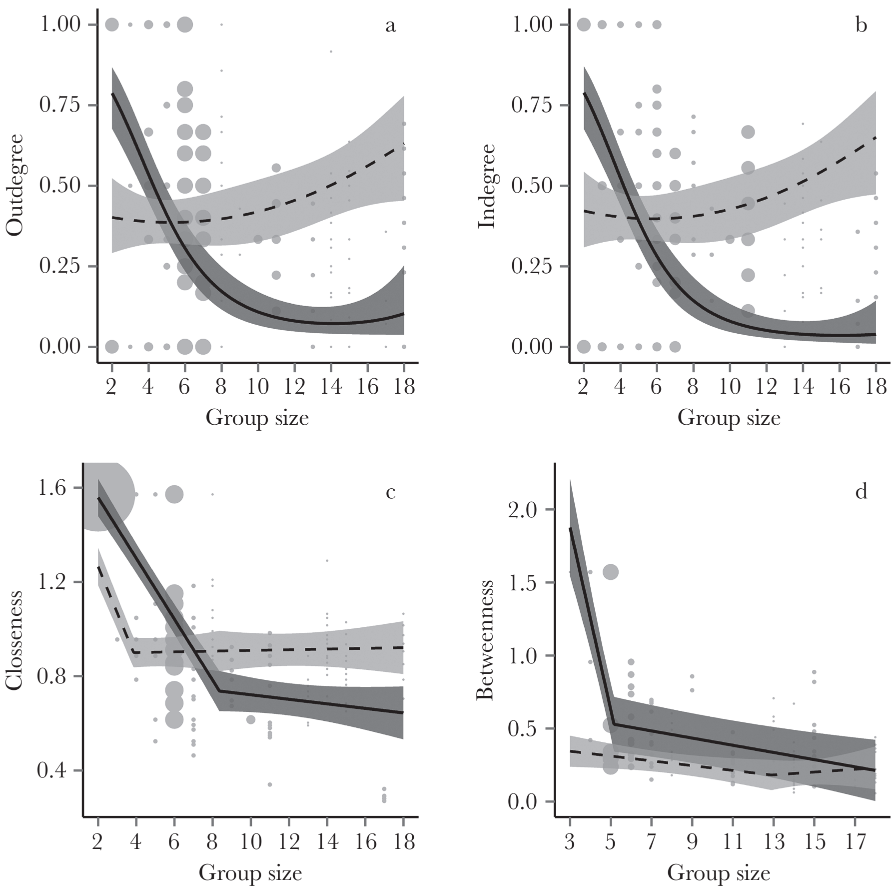

Figure 2
Results of the generalized linear mixed models explaining the variation in the 4 network measures in response to changes in female marmot groups. Black solid lines illustrate the regression line fitted with the observed network attributes. The confidence intervals are denoted as a gray shaded polygon. Dark gray dashed lines illustrate the regression line fitted with the social attributes calculated from Erdös–Rényi random networks ($P = 0.5$). Confidence intervals are denoted as a light gray shaded polygon. (a) Fitted line of the outdegree response and raw data, (b) fitted line of the indegree response and raw data, (c) fitted line of the closeness response and raw data, and (d) fitted line of the betweenness response and raw data. Circles: aggregated values of each of the raw social network measures.

Likewise, the probability that an individual received more social interactions decreased at an average of −0.393 (SE = 0.044; $P < 0.001$) and then, for groups larger than 10, increased at an average of 0.023 (SE = 0.008; $P = 0.003$) social partners per additional individual (Figure 2b). Yearlings were more likely to receive more ties as group size increased than adults (0.710; SE = 0.264; $P = 0.007$). Our indegree model explained 39.77% of the variance.

Closeness centrality significantly decreased at a rate of −0.129 (SE = 0.009; $P < 0.001$) per additional individual. The slope significantly changed from a steep to gradual decrease around a group size of 8 individuals. After this break point, closeness centrality did not significantly change (−0.009; SE = 0.007; $P < 0.001$) as a function of increased group size (Figure 2c). Yearlings were significantly closer to other members of the group than adults (0.107 ± 0.030; $P = 0.007$). The closeness model explained 55.51% of the variance.

Finally, betweenness centrality decreased quickly at small group sizes (−0.950 ± 0.127; $P < 0.001$; Figure 2d) and then it decreased at lower rates for larger groups (>5 individuals) (−0.03 ± 0.008; $P < 0.001$; Figure 2d). Yearling and adults did not significantly differ in their betweenness (0.014 ± 0.043; $P = 0.747$). Our betweenness model explained 74.33% of the variance.

The observed reaction norms for our social attributes indegree, outdegree, and closeness differed from that expected by chance (Figure 2a–c). In other words, compared to a random process, marmots were significantly more social at small group sizes. However, as group size increased, marmots were significantly less likely to initiate or receive connections or to have more central positions than expected by chance. For betweenness, there were significant deviations from random for groups smaller than 8 but not for larger groups (Figure 2d). In other words, for small group sizes, betweenness centrality decreased at a significantly faster rate than expected by chance, but this trend disappeared as group size increased.

DISCUSSION

Specific attributes of yellow-bellied marmot social relationships are correlated with group size: marmots were less likely to add or receive new social partners as group size increased, and their closeness and betweenness centralities decreased with increases in group size. Thus, our results show that marmots are behaviorally flexible and can adjust their social behavior to variation in their social environment. Moreover, many of the identified patterns of behavioral plasticity differed from those expected by chance, suggesting that there are individual-level mechanisms that allow marmots to balance the costs and benefits of maintaining social relationships. This suggests that the flow of information and/or disease may be affected by the behavioral decisions made by individuals within a group. Our results also indicated that age is a potentially important factor that influences sociality. Yearlings are more interactive (i.e., they had a higher indegree and closeness) than adults, a finding that supports previous research that showed that younger individuals are more sociable and have a potentially important role in maintaining social cohesion (Wey and Blumstein 2010).

Although our observed patterns supported the existence of behaviorally plastic responses, the comparisons between the observed and the random patterns suggested that when there were nonsignificant differences, some elements of the emergent properties of social behavior at the group level may be explained by alternative mechanisms that follow random processes. For example, in house mice (*Mus domesticus*), and in red foxes (*Vulpes vulpes*), random processes explain aspects of their spatial and social behavior (Giuggioli et al. 2011; Perony et al. 2012). We know, however, that animals often interact nonrandomly with group members (Kurvers et al. 2014). Thus, significant differences between the emergent patterns of behavioral plasticity and the random expectations suggest the existence of behavioral rules that govern social interactions.

The ability of marmots to behaviorally respond to changes in their social environment may imply that individuals are able to evaluate the costs and benefits of socially interacting under different circumstances and avoid the costs of increased sociality. Our analyses show that at small group sizes, individuals apparently work to increase social interactions. Interestingly, as group sizes increases, individuals either behave randomly or seem to avoid participating in more social interactions. This may be a mechanism to avoid the costs of increased sociality.

The rate of decline in the likelihood of making new social partners as group size increased suggests that sociality in female yellow-bellied marmots may entail net costs, such as increases in within-group competition, spread of parasites, or possibly reproductive suppression (Alexander 1974; Krause and Ruxton 2002; Silk 2007a). For example, in long-tailed macaques (*Macaca fascicularis*), intraspecific competition may reduce individual food intake and therefore increasing group size creates more costs than benefits (van Schaik and van Noordwijk 1986). Alternatively, individuals may choose to selectively interact with few individuals in the group, implying the existence of social preferences among members of a group (Lehmann and Boesch 2009) that may reduce the cost of group living. In marmots, such preferences may emerge as a result of the kinship structure that influences the affiliative networks (Wey and Blumstein 2010). Furthermore, restricting the number of individuals one interacts with may also be an adaptation to minimize the spread of contact-transmitted diseases and parasites by reducing the frequency of direct contact with potentially infected individuals (i.e., decreasing infection risk). This may be the case in yellow-bellied marmots, where parasite load does not always increase with group size (Lopez et al. 2013), thus suggesting that social species may have acquired an adaptation to prevent the spread of parasites in large groups (Bordes et al. 2007). Therefore, as group size increases, the trade-off between the benefits and costs of sociality may determine the number, strength, and nature of the social relationships among group members.

The decay in closeness values suggests that there may be an inevitable loss of control over other members of the group as group size increases. Therefore, females in larger groups have less influence over other individuals in their group. This has implications for dominance relationships in larger groups. As individuals lose control, a single individual may not be able to exert dominance over others. This might have practical demographic consequences if this means that formerly dominant individuals are unable to suppress reproduction of other females. Additionally, most animals have no calculable betweenness, perhaps because females within a group occupy more peripheral positions in the network. By contrast, marmots with betweenness centrality values greater than 0 may serve as links between individuals that are not directly connected, or between subgroups within a social group, as has been described in bottlenose dolphin (*Tursiops* spp.) networks (Lusseau and Newman 2004).

Taken together, our results paint a rather simple picture of female marmot sociality, which in some ways is similar to male marmot sociality (Olson and Blumstein 2010). The lack of social complexity may be a product of proximate mechanisms such as temporal and cognitive constraints that limit the number of social relationships that an individual can maintain (Dunbar 1992b; Lehmann et al. 2007; Pollard and Blumstein 2008; Sueur et al. 2011; Blumstein 2013), thus affecting the social structure. Individuals must distribute their time among various activities (foraging, vigilance, travel, etc.), meaning that individuals are limited in the time that they may allocate to social activities (Mitani 1989; Dunbar et al. 2009). Alternatively, the neocortex size limits the amount of information that an individual can process, which therefore limits the number of social relationships that an individual can monitor (Dunbar 1992a; Lehmann et al. 2007). Therefore, individuals in a group are seemingly limited in the number of social relationships that they can maintain.

Sociality is a key factor that affects the survival and reproduction of social species. We have shown that animals seemingly adjust the specific nature of their social relationships according to changes in their social environment. Such behavioral plasticity may alter the interaction between behavior and sociodemography, which in turn can affect population dynamics (Calhoun 1952). As populations fluctuate both naturally and as a result of human impacts, it is important to understand the effects of these fluctuations on sociality in order to have a better insight of the role of sociality on the relationship between temporal environmental variation and population dynamics. Our statistical approach (i.e., reaction norms) to study behavioral plasticity can be widely applied to social species and, by doing so, may shed novel light on constraints on sociality.

SUPPLEMENTARY MATERIAL

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

FUNDING

A.M.-C. was supported by a Fulbright Fellowship. D.T.B. was supported by the UCLA Academic Senate and Division of Life Sciences, National Geographic Society, and National Science Foundation (NSF-IDBR-0754247 and NSF-DEB-1119660 to D.T.B.; and NSF-DBI 0242960, 0731346 to the Rocky Mountain Biological Laboratory).

We thank all the marmoteers who helped collect data. The comments of J. Fowler and several anonymous reviewers helped us improve previous versions.

Handling editor: Alison Bell

REFERENCES

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Evol Syst. 5:325–383.

Bates D, Maechler M, Bolker B. 2013. Linear mixed-effect models using S4 classes. R package version 0.999999-2 [cited 2014 April 24]. Available from: http://CRAN.R-project.org/package=lme4

Blumstein DT. 2013. Yellow-bellied marmots: insights from an emergent view of sociality. Phil Trans R Soc B. 368:20120349.

Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc R Soc B. 276:3007–3012.

Bordes F, Blumstein DT, Morand S. 2007. Rodent sociality and parasite diversity. Biol Lett. 3:692–694.

Bourke AFG. 1999. Colony size social complexity and reproductive conflict in social insects. J Evol Biol. 12:245–257.

Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv Genet. 13:115–155.

Butler RG. 1980. Population size social behavior and dispersal in house mice: a quantitative investigation. Anim Behav. 28:78–85.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35:1454–1469.

Calhoun JB. 1952. The social aspects of population dynamics. J Mammal. 33:139–159.

Crockett CM, Eisenberg JF. 1987. Howlers: variation in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RR, Struhsker TT, editors. Primate societies. Chicago (IL): The University of Chicago Press.

Croft DP, James R, Krause J. 2008. Exploring animal social networks. Princeton (NJ): Princeton University Press.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research. InterJournal Complex Systems, p. 1695.

Dingemanse NJ, Wolf M. 2013. Between-individual differences in behavioral plasticity within populations: causes and consequences. Anim Behav. 25:81–89.

Dunbar RI. 1992a. Neocortex size as a constraint on group size in primates. J Hum Evol. 22:469–493.

Dunbar RI. 1992b. Time: a hidden constraint on the behavioral ecology of baboons. Behav Ecol Sociobiol. 31:35–49.

Dunbar RIM, Korstjens AH, Lehmann J. 2009. Time as an ecological constraint. Biol Rev. 84:413–429.

Freeman LC. 1979. Centrality in social networks: I. Conceptual clarification. Soc Netw. 1:215–239.

Giuggioli L, Potts JR, Harris S. 2011. Animal interactions and the emergence of territoriality. PLoS Comput Biol. 7:e1002008.

Griffiths SW, Magurran AE. 1997. Schooling preferences for familiar fish vary with group size in a wild guppy population. Proc R Soc Lond B. 264:547–551.

Hinde RA. 1976. Interactions relationships and social structure. Man. 11:1–17.

Hovi M, Alatalo RV, Hoglund J, Lundberg A, Rintamaki PT. 1994. Lek centre attracts black grouse females. Proc R Soc Lond B. 258:303–305.

Kappeler PM, Barrett L, Blumstein DT, Clutton-Brock TH. 2013. Constraints and flexibility in mammalian social behavior: introduction and synthesis. Phil Trans R Soc B. 368:20120337.

Kappeler PM, van Schaik CP. 2002. Evolution of primate social systems. Int J Primatol. 23:707–740.

Koons DN, Pavard S, Baudisch A, Metcalf JE. 2009. Is life-history buffering or lability adaptive in stochastic environments? Oikos. 118:972–980.

Krause J, Lusseau D, James R. 2009. Animal social networks: an introduction. Behav Ecol Sociobiol. 63:967–973.

Krause J, Ruxton GD. 2002. Living in groups. Oxford: Oxford University Press.

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

Kuznetsova A, Brockhoff PB, Christensen RHB. 2014. lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). Version 2.0-6 [cited 2014 May 24]. Available from: http://cran.r-project.org/web/packages/lmerTest/index.html.

Lehmann J, Boesch C. 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. Anim Behav. 77:377–387.

Lehmann J, Korstjens AH, Dunbar RIM. 2007. Group size grooming and social cohesion in primates. Anim Behav. 74:1617–1629.

Lopez J, Wey TW, Blumstein DT. 2013. Patterns of parasite prevalence and individual infection in yellow-bellied marmots. J Zool. 291:296–303.

Lusseau D, Newman ME. 2004. Identifying the role that animals play in their social networks. Proc R Soc B. 271:S477–S481.

Maldonado-Chaparro AA, Martin JGA, Armitage KB, Oli MK, Blumstein DT. 2015. Environmentally-induced phenotypic variation in wild yellow-bellied marmots. J Mamm.

Mitani JC. 1989. Orangutan activity budgets: monthly variations and the effects of body size parturition and sociality. Am J Primatol. 18:87–100.

van Noordwijk MA, van Schaik CP. 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. Primates. 40:105–130.

Nussey DH, Wilson AJ, Brommer JE. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol. 20:831–844.

Olson LE, Blumstein DT. 2010. Applying the coalitionary-traits metric: sociality without cooperation in male yellow-bellied marmots. Behav Ecol. 5:957–996.

Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, Tuljapurkar S, Coulson T. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature. 466:482–485.

Perony N, Tessone CJ, König B, Schweitzer F. 2012. How random is social behaviour? Disentangling social complexity through the study of a wild house mouse population. PLoS Comput Biol. 8:e1002786.

Pigliucci M. 2001. Phenotypic plasticity: beyond nature and nurture. Baltimore (MD): Johns Hopkins University Press.

Pollard KA, Blumstein DT. 2008. Time allocation and the evolution of group size. Anim Behav. 76:1683–1699.

R Core Team. 2014. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: www.r-project.org.

Rosvall M, Axelsson D, Bergstrom CT. 2009. The map equation. Eur Phys J Spec Top. 178:13–23.

Rosvall M, Bergstrom CT. 2008. Maps of information flow reveal community structure in complex networks. Proc Natl Acad Sci USA. 105:1118–1123.

van Schaik CP, van Noordwijk MA. 1986. The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). Behavior. 99:296–315.

Schradin C. 2013. Intraspecific variation in social organization by genetic variation developmental plasticity social flexibility or entirely extrinsic factors. Phil Trans R Soc B. 368:20120346.

Silk JB. 2007a. The adaptive value of sociality in mammalian groups. Phil Trans R Soc B. 362:539–559.

Silk JB. 2007b. Social components of fitness in primate groups. Science. 317:1347–1351.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc B. 276:3099–3104.

Stearns SC. 1989. The evolutionary significance of phenotypic plasticity. Bioscience. 39:436–445.

Sueur C, Deneubourg JL, Petit O, Couzin ID. 2011. Group size, grooming and fission in primates: a modeling approach based on group structure. J Theor Biol. 273:156–166.

Takahashi DY, Sato JR, Ferreira CE, Fujita A. 2012. Discriminating different classes of biological networks by analyzing the graphs spectra distribution. PLoS One. 7:e49949.

Wasserman S, Faust K. 1994. Social network analysis: methods and applications. Cambridge (UK): Cambridge University Press.

West-Eberhard MJ. 1989. Phenotypic plasticity and the origins of diversity. Annu Rev Ecol Syst. 20:249–278.

Wey TW, Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. Anim Behav. 79:1343–1352.

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

Whitehead H. 2009. SOCPROG programs: analyzing animal social structures. Behav Ecol Sociobiol. 63:765–778.

Wood S, Scheipl F. 2013. gamm4: generalized additive mixed models using mgcv and lme4. Version 0.2-2 [cited 2014 May 24]. Available from: http://cran.r-project.org/web/packages/gamm4/index.html.