

**Exploring the behavioral rules influencing sociality in a facultatively social species, yellow-
bellied marmots (*Marmota flaviventris*)**

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9 **ABSTRACT**

10 From fish schools and bird flocks to mammal herds and insect swarms, many animal species can
11 be found in social groups, where they are guided by simple ecological rules and behavioral
12 mechanisms that influence their decision to interact with others. While there is considerable
13 literature on the emergence of animal social complexity, most of these available works tend to
14 emphasize the study of obligately social species. Thus, this project served as a modeling exercise
15 to explore the rules influencing sociality in a facultatively social species, the yellow-bellied
16 marmot (*Marmota flaviventris*). In particular, we considered the effects of seven homophily-type
17 interactions—age, sex, relatedness, and their combinations—on social network structure in these
18 animals. Using social interaction data collected from a long-term study of individually marked
19 marmots at the Rocky Mountain Biological Laboratory (RMBL) in Colorado, we built
20 association matrices and calculated five social network measures—degree, closeness, strength,
21 clustering coefficient, and average path length—that were compared to simulated results.
22 Experimental data came from the individual-based or agent-based modeling of marmot colonies
23 using the program NetLogo.

24

25 **Keywords:** emergent properties, homophily, individual-based modeling, social networks,
26 yellow-bellied marmots

INTRODUCTION

For years, the emergence and development of complex animal social behavior has been one of the most widespread and discussed topics among ecologists and evolutionary biologists. Current views hold sociality as a multifaceted continuum of interactions, ranging from simple and temporary aggregations to highly organized and structured social groups (Lott 1984). Such attractions between individuals lead to increasing levels of communication, cooperation, and coordination that allow for new patterns of self-organization and collective decision-making to emerge. Consequently, simple ecological rules (Morrell and James 2008) and behavioral mechanisms (Peterson 1993) play a large role in establishing these groups, affecting both their formation and composition. Furthermore, once in groups, many animals may then find themselves subject to additional intrinsic and extrinsic factors that influence their decision to interact with others (Croft 2008).

Standing at the foundation of social animal behavior are lower complexity phenomena, such as the establishment of groups and their coordination (Hemelrijk 2013). While aggregations may differ considerably in qualities such as size, longevity, and heterogeneity, their formation relies on two processes: social attraction and environmental variation (Hemelrijk 2013). Attractions are often mediated through visual cues, as can be seen in seabirds like Laysan albatross (*Diomedea immutabilis*) (Arnold et al. 2011) and fish like striped mullet (*Mugil cephalus*) (Olla and Samet 1974), as well as chemical cues, including those seen in beetle larvae (---) (Camazine et al. 2001) and Luschan's salamander (*Mertensiella luschani*) (Gautier et al. 2006). Groups can also form solely through environmental causes (Hemelrijk 2013). Such systems are commonly the result of varying distributions in food, such as in spider monkeys (*Ateles geoffroyi*) (Ramos-Fernández et al. 2006); degrees of habitat availability, like in large

mammalian herbivores (Estes 1974; Evans 1979; Hillman 1987); and the presence of predators, including those observed in banded killifish (*Fundulus diaphanus*) (Hoare et al. 2004). Once in groups, social animal species are able to use simple rules and mechanisms of collective decision-making to engage in various levels of group coordination during travelling, foraging, and habitat selection. Instances of this type of behavior are abundant when studying colonies of army ant (*Eciton burchellii*) (Deneubourg and Goss 1989), swarms of locusts (Buhl et al. 2006), herds of ungulates (Gueron et al. 1996), schools of fish (Couzin et al. 2002; Hemelrijk and Kunz 2005; Huth and Wissel 1992, 1994; Kunz and Hemelrijk 2003), and flocks of birds (Hildenbrandt et al. 2010; Reynolds 1987; Hemelrijk and Hildenbrandt 2011, 2012).

Such simple forms of group living can promote and eventually reinforce stable and predictable interactions that result in greater levels of order and higher complexity phenomena concerned with how individual differences influence group social structure (Hemelrijk 2013). This emergent process of increasing social complexity within animal species has resulted in the development of self-organization and rules for interaction. Varying levels of aggression among group members, for example, have been shown to foster the establishment of dominance hierarchies and contribute to individual rankings within group units in species such as domestic goats (*Capra hircus*) (Barroso et al. 2000) and male capybaras (*Hydrochaeris hydrochaeris*) (Herrera and MacDonald 1993). Individual personality types can also greatly affect the social structure of the group, as can be observed in great tits (*Parus major*) (Verbeek et al. 1999), where bold individuals rise in dominance ranking while cautious individuals have relatively lower standing, as well as in populations of three-spined sticklebacks (*Gasterosteus aculeatus*) (Pike et al. 2008) and Trinidadian guppies (*Poecilia reticulata*) (Croft et al. 2009), where behavioral differences in boldness between individuals affected the frequency and distribution of

their interactions within a network. Allocation of affiliative behavior, on the other hand, can produce social relationships that serve as the basis for more complex social networks, like in the case of adult female vervet monkeys (*Cercopithecus aethiops*), which have been known to engage in altruistic grooming in exchange for support and alliances (Seyfarth 1980). Stable relationships may even permit the development of habitual roles and task division, such as in plains zebras (*Equus burchelli*), where integrated bonds and social ties influence leadership roles (Fischhoff et al. 2006), and most notably social insects including bumblebees (*Bombus terrestris*) (Hogeweg and Hesper 1983, 1985).

As noted above, the literature available on animal aggregation and sociality is staggering. However, many of these studies tend to focus primarily on obligately social species, especially highly integrated species, such as primates, carnivores, and ungulates. Limited progress has been made on observing the parameters determining group formation and sociality in facultatively social vertebrates. Thus, we aimed to explore the putative rules that influence social interaction and hence social structure in a facultatively social species, the yellow-bellied marmot (*Marmota flaviventris*). Specifically, we investigated the consequences of the homophily principle (McPherson et al. 2001) on marmot network dynamics by analyzing how constraints on age, sex, and relatedness between interacting individuals affected network structure. A basic organizing concept, homophily refers to the tendency for similar individuals to associate and form ties, thus limiting their social worlds and altering the information they receive and the interactions they experience (McPherson et al. 2001). While homophily has been widely studied in many human social networks (McPherson et al. 2001; Newman 2003), this social phenomenon can also be found as a possible mechanism of network formation in animal systems (Lusseau and Newman 2004; Croft et al. 2005; Wey and Blumstein 2010; Massen and Koski 2014).

In particular, we hoped to explain how yellow-bellied marmots decide whether or not to be social and interact with others. We addressed this idea by studying factors that influence biases in social interactions because it is through these biased interactions that different social relationships emerge. To investigate the effects of social conditions on group structure and social interactions, we employed an individual-based or agent-based modeling approach, which allowed us to explore how local interactions between different marmots influenced global properties, specifically colony social network structure (DeAngelis and Grimm 2014). This proved especially useful in examining how individual responses to defined changes affected variations in the tendencies of marmots to form groups and interact with others at the local level (Thiele 2014). The long-term goal of this research was to investigate the rules that allow individuals to live and interact in groups, and to create models that capture the social mechanisms under which these animals create relationships and form social networks. In the process, we also sought to investigate the amount of complexity necessary for a social system to accurately and consistently reflect real-world social interaction patterns.

We conducted our study based on complexity theory, which explains how populations can self-organize into aggregations that generate patterns of social behavior, store information, and engage in collective decision-making as a consequence of individuals interacting with their social or physical environment (Parrish and Edelstein-Keshet 1999; Hemelrijk 2002). Indeed, models have shown that the interactions of an individual with others and its environment can lead to traits that are emergent, such as the shape of a fish school, the specific swarming pattern in ants, and the centrality of dominant primates (Hemelrijk 2013). Application of complexity theory further describes specific group attributes, such as social network structure, as emergent properties generated by behavioral mechanisms that guide the social interaction decisions of

group members. In other words, simple behavioral mechanisms at the level of the individual can result in complex social interaction patterns at the group level (Hemelrijk 2002). Thus, we hypothesized that marmots follow simple rules of social behavior that allow them to decide whether or not to interact with a nearby individual. Ultimately, by testing our assumptions of the factors that define variation in social groups and determine interaction decisions between group members, we sought to provide a more comprehensive picture of how ecological and social factors act to change behavioral conditions and social tendencies in a facultatively social species.

METHODS

Study system

We studied a population of free-living yellow-bellied marmots around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (latitude 38° 57' 29" N; longitude 106° 59' 06" W), where they have been observed since 1962 (Blumstein 2013; Armitage 2014). Marmots are a facultatively social species of sciurid rodents that hibernate from September/October to April/May and rely on the establishment of basic social units called matriline (Armitage 1991, 1998). The occupation of one or more of these matrilineal units in a single habitat patch constitutes a colony. However, there is considerable social variation within these social groups, as not all members interact in the same way, and not all interact in more complex social networks (Maldonado-Chaparro et al. 2015).

Social groups are generally based on female kinship, specifically mother:daughter:sister relationships (Armitage 2014). Marmots are also harem polygynous in that a single territorial adult male typically defends and monopolizes a colony, although multiple males may sometimes tolerate each other (Armitage 1991; Olson and Blumstein 2010). As a consequence of this

organization, social complexity in these animals has been suggested to depend on variations in sex (Armitage 1974), age (Blumstein 2013), and relatedness (Armitage 2007, Blumstein 2013) between group members.

Behavioural observations and demography

Marmots were systematically live-trapped and observed from 2002 to 2014. At each trapping event, we recorded the mass (in grams), sex, and reproductive status (categorized as non-reproductive, nipples, prominent, nipples swollen or lactating; Armitage and Wynne-Edwards 2002) of each captured animal. Individuals were classified into one of three age categories: pups (<1 year old), yearlings (1 year old), or adults (≥ 2 years old). Pups were usually caught within one week of emergence from their natal burrow. Individuals trapped for the first time were also given a pair of permanent numbered ear tags and all marmots were uniquely marked (or re-marked) with black non-toxic Nyanzol fur dye on their dorsal pelage for identification and observation from afar.

In addition to live trapping, we quantified social interactions using an all occurrence sampling scheme (details in Blumstein et al. 2009) throughout the entire active season, from mid-April to early September. Observations were made during periods of peak marmot activity (07:00-10:00 hours and 16:00-19:00 hours; Armitage 1962) and from distances that did not interfere with normal behaviour (20-150 meters). For each social interaction, we noted the type of behaviour (affiliative or agnostic), the initiator and recipient, and the time and location at which the behaviour took place (Blumstein et al. 2009). Affiliative interactions included allogrooming, greeting, sitting in body contact and in close proximity, foraging together within 1

meter, and play behaviours. Agonistic interactions included aggressive behaviours and displacements. Equivocal interactions were removed from the dataset.

Individual-based modeling

To identify the social conditions influencing group structure and interactions in marmots, we created individual-based modeling experiments using NetLogo, a programmable tool used to simulate environmental and social phenomena (Wilensky 1999). This model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, 2010).

1. Purpose

The purpose of the model is to uncover the simple behavioral rules that guide social interactions in yellow-bellied marmots (*Marmota flaviventris*), a facultatively social rodent species. By exploring the social homophily biases that influence marmots to develop greater levels of sociality and establish more complex networks, it aims to build upon basic principles of animal social complexity and provide richer representations of real-world scenarios. The model is based on the idea that simple rules of interaction between individuals can lead to complex emergent properties characteristic of the entire group, such as social network structure. In addition to better understanding the behavioral mechanisms underlying sociality in this species, the model also seeks to reveal the level of complexity necessary for marmot social systems to express the organization and diversity of network interactions observed in the field.

2. Entities, state variables, and scales

Agents/individuals. Marmots are the only type of agent included in the model. Each marmot is characterized by a set of randomly assigned properties or state variables. All individuals have a unique identification number (provided by NetLogo), age (in years), age-category (yearling or

adult; pups were not included), sex (male or female), relatedness coefficient ($r=0-1$, with $r \geq 0.50$ meaning highly related), location (grid cell), and interaction probability (calculated based on age, 0.117 for yearlings and 0.129 for adults). Size (1 pixel for yearlings, 1.5 pixels for adults) and color (35 for females and 34 for males) are also provided to visually distinguish between individuals of different ages and sexes within the NetLogo model interface.

Spatial units. Grid cells in the model are 18.7 pixels in size and produce a 32x24 representation of a one of our main colony sites at the Rocky Mountain Biological Laboratory (RMBL), Marmot Meadow (Figure 1). One grid cell represents 10 meters and the model landscape comprised 32x24 meters. Each of spatial units had two state variables: individual count and burrow location. Individual count provides a list of agents within a cell, with the sum of all cell individual counts representing the total number of marmots, or the colony size. Burrow location refers to spatially distinct patches that served as marmot burrows. Each burrow takes up one to four grid cells, is randomly located within the environment, and has a distinguishable color (red, blue, yellow, or violet). A total of four burrows are included in the model.

Temporal units. One time step represents one day and simulations are run for 110 days, the average number of days observed at Marmot Meadow in an active season.

Collectives. The collective in the model is characterized by a list of all the marmots created in the environment, which we referred to as the colony. The demographic composition of the colony serves as the foundation for which we are able to determine interaction tendencies and social network structure.

3. Process overview and scheduling

In each time step, marmots have the opportunity to participate in a *social interaction*. Every individual randomly chooses one or more other individuals to link with. Depending on the

210 behavioral rules presented, marmots then have a calculated probability of actually interacting
211 with their designated partners. After marmots decide whether or not to interact, their social
212 memory is updated, which acts as a list that keeps track of all the individuals with which the
213 focal animal interacted with during the specified time step.

214 **4. Design concepts**

215 Basic principles. This model relies on previously developed theories of complexity science and
216 the concept of emergence (Christen and Franklin 2002), the scope of which reaches the system
217 level. The experimental simulations included in the model also further extend the idea of the
218 homophily principle (McPherson et al. 2001).

219 Emergence. The social network structure of the colony emerge from interactions among the
220 individual marmots.

221 Sensing. Marmots have complete information of their partners' age, sex, and relatedness
222 coefficient. Individuals are simply assumed to know these state variables, rather than have such
223 mechanisms modeled explicitly.

224 Interactions. Pairs of marmots have varying probabilities of interaction depending on each
225 participant's age, sex, and relatedness. The kinds of interactions that occur between agents are
226 influenced by basic age differences or age-rate (yearlings interact more than adults), age
227 homophily (individuals of the same age are more likely to interact than individuals of differing
228 ages), sex homophily (individuals of the same sex are more likely to interact than individuals of
229 opposite sexes), relatedness homophily (kin members are more likely to interact than unrelated
230 individuals), and combinations of those aforementioned homophily types—age-sex homophily,
231 age-relatedness homophily, sex-relatedness homophily, and age-sex-relatedness homophily. All

interactions in the model are considered direct interactions, in which individuals encounter and affect others.

Stochasticity. Modeled processes that are assumed to be random include the choosing of interaction partners for each marmot involved in the simulation. Stochasticity allows us to reproduce variability in interactions similar to those in the real world, and to cause model behaviors to occur with a specified frequency.

Collectives. Marmots belong to social groups called colonies. Each model simulation contains one colony composed of all the marmots created during the experiment run.

Observation. A list of social interactions is collected from the model for testing and analysis. This list is composed of the social memories of all the marmots involved in the model, and is used to create association matrices for studying relationships.

5. Initialization

24 different simulations are run 100 times each, with 5, 15, or 25 individuals, correlating to group size conditions at Marmot Meadow in 2002, 2011, or 2008, respectively. For each of these three years, eight experiments are used to test the influence of homophily interactions in developing social network structure. The first experiment serves as a null, where all interaction types have the same inherent probability of occurring as a result of age rate. The next three experiments bias simple homophily interactions, particularly those concerned with age, sex, and relatedness. The last four experiments evaluate the influence of more complex homophily interactions on marmot networks, including those examining both age and sex, age and relatedness, sex and relatedness, as well as age, sex, and relatedness.

Of the individuals initially set up, 20.3% are female yearlings, 22.5% are male yearlings, 35.6% are female adults, and 21.7% are male adults. Average age-sex structure percentages were

calculated from live-trapping and observation logs that contain information for every marmot seen at least once from 2002 to 2014. Based on their age and sex, all marmots are also assigned a size and color, in addition to a random relatedness coefficient, before being arbitrarily distributed over the model environment, which has been colored green (53+3) and set up with four distinct burrow locations.

6. Input data

In order for our model marmots to parallel the social patterns of the live marmots we observed at RMBL, we used social interaction data collected from 2002 to 2014 to calculate the average daily interaction probabilities for the different interaction types included in the model. Probabilities of homophily (P_x), non-homophily (P_y), and age-rate (P_z) interactions, were all calculated using this equation:

$$P = \frac{(i/n)}{d}$$

where P is the daily interaction probability, i is the number of interactions of a specific type, n is the number of possible interactions of that type (measured as a permutation of the number of individuals involved) and d is the number of observation days in a given year. Interaction probabilities were computed for each Julian date of each recorded year at Marmot Meadow and then averaged accordingly (refer to Table 1 for values).

Calculating interaction probabilities involving relatedness also required genetics data, which contain loci information for every marmot studied at RMBL since 1962. Using this database and KINGROUP v2.0, a program for pedigree relationship reconstruction and kin group assignment using genetic markers (Konovalov et al. 2004), we estimated pairwise relatedness coefficients (r) for each pair of marmots included in our social interaction observations dataset.

7. Submodels

Social interaction. In social interaction, a focal agent, the caller or initiator individual, is linked with another randomly chosen agent, the recipient individual. The likelihood of the pair to interact is then determined, depending on the homophily type being considered. If both initiator and recipient are of the same age, sex, relatedness, etc. they have a $P_x \times P_z$ probability of interaction, corresponding to the probability of a particular homophily type interaction occurring multiplied by the probability of interaction based on age. Otherwise, the pair has a $P_y \times P_z$ probability of interaction, corresponding to the probability of the non-homophily type interaction occurring multiplied by the probability of interaction based on age. When no interaction is made between the pair, however, the link dies.

Update social memory. In update social memory, a focal agent's memory of social interactions is updated with its most recent linked partners. If an individual chooses not to interact during a given day, a blank entry is added to its social list as a placeholder.

Quantifying social relationships

From our model outputs and observed social interaction data, we constructed adjacency matrices to reflect the interaction patterns of both our model marmots and our observed marmots. With igraph package v0.7.1 (Csardi and Nepusz 2014), we produced separate asymmetrical matrices based on affiliative and agonistic interactions between individuals at Marmot Meadow from 2002 to 2014. In each case, matrices were constructed for males and females (yearlings and adults) within the social group. Pups were not included in this study.

Social network analysis then allowed us to measure specific social attributes and determine social structure at individual, intermediate, and group levels (Wey et al. 2008). For our analyses, we created affiliative and agonistic social networks from our interaction matrices using

igraph package v0.7.1 (Csardi and Nepusz 2014). Depending on each parameter we defined, our ties were either directed or undirected, and weighted or unweighted. Directed ties refer to interactions that specify the initiator and recipient in a relationship. This property of network directionality is particularly useful for asymmetric matrices, where potential inequality may exist. In some instances, ties were also weighted. Weighted ties not only determined whether a connection existed between two individuals, but also revealed the strength or magnitude of that relationship (Wey and Blumstein 2010).

We used a set of five social network measures—degree, closeness, strength, clustering coefficient, and average path length—to characterize the consequences of individual-based interactions on group-level attributes. *Degree centrality* is defined as a local measure of the number of direct connections an individual has, with in-degree (reception) signifying interactions received and out-degree (emission) representing interactions initiated (Wey et al. 2008). Calculations of in- and out-degree rely on summing the number of ties terminating and originating, respectively, from a focal subject (Wasserman and Faust 1994). To quantify degree, we converted our matrices to directed, unweighted networks. *Strength* measures the magnitude of a relationship (Barthélemy et al. 2005), and is calculated as the number of times an individual receives or initiates an interaction with another individual (Barrat et al. 2004). *Closeness centrality* corresponds to the shortest-path distance from one individual to all other members of a group (Wey et al. 2008), and can be found as the reciprocal sum of shortest path lengths between a focal subject and everyone else (Wasserman and Fause 1994). *Clustering coefficient* is considered an intermediate measure that examines the density of subgroups within a network, and is calculated by dividing the actual number of ties between neighbors with all possible tie combinations between those same neighbors (Wey et al. 2008). As a measure of cohesiveness,

we analyzed clustering coefficient in reference to directed and unweighted networks. *Average path length* is a group measure that takes into account the average of all path lengths, or the shortest number of ties, between pairs in a network (Wey et al. 2008). We converted our matrices to undirected, unweighted networks to quantify clustering coefficient and average path length; directed, unweighted networks for degree and closeness; and directed, weighted networks for strength. Individual attributes were calculated separately for affiliative and agonistic interactions, and in combination, to provide a more comprehensive understanding of social relationships.

Statistical analyses

To measure the correlation between our experimental matrices and observed matrices, we performed Mantel tests (Mantel 1967; Schnell et al. 1985) using the Pearson correlation method from vegan package v2.2-1 (Oksanen et al. 2015). This procedure examines the relationship between two similarity (or dissimilarity) distance matrices by permuting the identities of the individuals in one matrix many times and calculating the matrix correlation coefficient for each permutation, indicating the overall degree of association between the two measures (Whitehead 2008). Mantel statistical r values for each run of a given experiment were then used to construct histogram distributions, allowing us to determine the underlying correlative structure that exists between an observed matrix and the set of 100 matrices produced by each experiment. Resulting graphs with narrow distribution spreads centered near $r = 1$ suggested higher correlations.

In addition to analyzing matrices, we also compared observed and experimental social network measures using two different methods depending on the level at which each measure acted upon. For the group measure, average path length, we constructed boxplots based on the multiple runs performed for each homophily type experiment of every year in study. The average

path length value calculated from a particular year's observed matrix was then plotted on top of the produced boxplot. Observed values within the range of the confidence interval suggested a greater agreement with model values, and thus a higher correlation between observed and experimental social networks. For local measures, degree centrality, closeness centrality, and strength, we first ran a Welch two-sample t-test for each run of each homophily type experiment. The resulting t-statistic values were then used to plot a histogram, where a positively skewed distribution below $t=2$ supports our null hypothesis that the populations from which the samples have been drawn are identical. As an intermediate measure, clustering coefficient was analyzed using both group- and individual-level methods. All analyses were implemented in R v3.1.2 (R Core Team 2014).

Ethics statement

Marmots were studied under University of California Los Angeles Institutional Animal Care and Use protocol (2001-191-01; renewed annually), and under permits from the Colorado Division of Wildlife (TR917, issued annually). During the course of this study, marmots were captured and handled. Individuals were in the traps no longer than three hours (usually less), and were released at the site of capture after manipulation, which typically lasted less than ten minutes depending on the type of data collected. All marmots were handled while inside a cloth handling bag to reduce stress and prevent injuries during processing.

RESULTS

Based on social interaction observations, we followed a colony from Marmot Meadow in three separate years: 2002, 2008, and 2011 (Table 2). From these individuals, we took into account a

total of 21 affiliative interactions in the first year (68 days), 462 interactions the next year (110 days), and 1672 interactions the final year (115 days). In comparison to observed data, our experiments produced one of three colonies, in which each model social group parallels the age-sex demographic of the Marmot Meadow colony in one of the three years in study (Table 3). Interactions varied with each experimental run.

Correlation between association matrices

When testing the correlation between affiliative social interaction matrices constructed from observational and experimental data, we found no associations regardless of group size or homophily bias (Figures 2, 3, 4).

Comparison of social network measures

For average path length of affiliative interactions, no observed values were within the confidence intervals established by the experimental calculations for any homophily type experiment (Figure 5). In terms of local measures, t-distributions representing affiliative strength appeared to exhibit the greatest level of similarity between the model and observed population from Marmot Meadow in 2002, especially with respect to sex and age-sex homophily (Figures 6c, 7e). None of the other experimentally calculated social factors from 2002, 2008, or 2011 demonstrated any significant degree of similarity when tested against observed values (Figure 6, 7, 8). While t-distributions for the intermediate measure, clustering coefficient, did not reveal model and observed populations to be significantly similar to each other (Figure 9), the distribution of clustering coefficients calculated from experimental runs based on age homophily for Marmot Meadow in 2002 did contain one observed value within its confidence interval at $x = 0.972$

393 (Figure 12b). No other plots suggested strong correlations between experimental and observed
394 clustering coefficient values (Figures 10, 11, 12).

PLEASE NOTE:

Data collection and analysis still need to be performed for agonistic social interactions between individuals at Marmot Meadow in 2002, 2008, and 2011. Until then, the results and discussion sections of this paper cannot be completed.

I will continue to work on this project with my mentors, Dan Blumstein and Adriana Maldonado-Chaparro, when I return to UCLA. In the next few weeks, I will be calculating social probabilities for agonistic interactions and running homophily experiments in NetLogo to produce model social interaction outputs. With this data collected, I will proceed by building association matrices and calculating social network measures (degree centrality, closeness centrality, strength, clustering coefficient, average path length). This will then allow me to analyze the correlation between experimental and observed matrices using the Mantel test, as well as compare social network measures via two-sample independent t-tests. All tables and figures will also be added to the research paper at this point as well.

Once all necessary statistical analyses have been completed, I will discuss the comprehensive results obtained from both affiliative and agonistic social interactions with Dan and Adriana to reach a better understanding of our findings.

412 **DATA ACCESSIBILITY.** Data are available at
413 <https://www.eeb.ucla.edu/Faculty/Blumstein/MarmotsOfRMBL/data.html>.

414

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421

422 **AUTHOR CONTRIBUTIONS.** WJY ran the individual-based models, carried out the social
423 network statistical analyses, and drafted the manuscript. AMC and DTB coordinated the study,
424 revised the manuscript, and collected live-trapping and observation data. All authors participated
425 in the design of the study and the interpretation of results.

426

427 **CONFLICT OF INTEREST.** The authors declare no competing interests.

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