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Los Angeles

Causes and consequences of variation in social network attributes
in yellow-bellied marmots (*Marmota flaviventris*)

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requirements for the degree Doctor of Philosophy
in Biology

by

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ABSTRACT OF THE DISSERTATION

Causes and consequences of variation in social network attributes
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Enormous variation exists in animal sociality, and understanding the evolution and maintenance of this variation is one of the major themes in behavioral ecology. Interaction among group members is often a major component of social living, yet detailed studies of the causes and consequences of social interactions are relatively rare. Network analysis offers a broad framework for studying patterns of interactions, but its general utility remains to be tested in animal systems. My dissertation work explores social network analysis as a general methodology for studying animal behavior and applies it to examine biological causes and

consequences of individual social attributes in yellow-bellied marmots (*Marmota flaviventris*). I first reviewed existing network literature in many fields of study and discuss potential applications and limitations for social network analysis in animal behavior. The network approach has the strengths in providing quantifiable measures of social attributes at multiple levels of analysis, and if applied properly, can offer diverse insights into animal social behavior. Next, I examined the ontogeny of individual social attributes and the role of age, sex, and kinship in structuring marmot social networks. Patterns of development in affiliative and agonistic attributes with age indicate that younger marmots contribute more to maintaining social cohesion, while older marmots play a more prominent role in competitive networks. Additionally, affiliative networks were significantly structured by age and kinship, suggesting that these factors strongly shape marmot social structure. Finally, I tested hypotheses about the relationship between individual social attributes and multiple fitness measures (annual reproductive success, number of ectoparasites, diversity of endoparasites, and basal stress). In general, there were more benefits than costs associated with high attribute values for both affiliation and agonism, implying a large potential adaptive value of sociality even in this facultatively social species. However, patterns of association varied considerably between age-sex groups, indicating that the adaptive value of sociality changes with life stage and differs between females and males. In marmots, attributes measuring absolute amounts of direct interactions had more

observable fitness correlates than attributes measuring indirect interactions or relative amounts of interaction. Overall, this network attribute-based approach was revealing in marmots and should also have broad utility across other animal systems.

CHAPTER 1

GENERAL INTRODUCTION

Animal sociality is a widespread, diverse, and complex phenomenon, and understanding the evolution and maintenance of social variation is a fundamental issue in behavioral ecology (Hamilton 1964, Alexander 1974, Smuts et al. 1987, Dugatkin 1997, Krause & Ruxton 2002, Wolf & Sherman 2007). Theory predicts and evidence confirms that there are both benefits and costs to social living across numerous dimensions (Alexander 1974, Krause & Ruxton 2002). Fitness consequences may arise not only from group living per se but also from the resultant social behaviors and structure, and studying these facets in a meaningful way is crucial to an accurate and comprehensive understanding of sociality (Altmann 1974, Hinde 1976, Martin & Bateson 1993, Whitehead 2008).

Social behavior encompasses many distinct and measurable components, and focusing on components separately allows us to be precise about which contribute to observed outcomes. For example, Silk et al. (2003) demonstrated that social bonds, measured by a social index incorporating grooming interactions, contributed to female reproductive success in primates, independent of other social factors such as dominance or kinship. Though previously proposed, this effect could only be confirmed when variation in social bonds was measured precisely. However, behavioral ecologists typically limit themselves to a subset of relatively

simple measurements of sociality that do not directly measure behavior or interactions, such as group living or group size (Brown & Brown 1996, Krause & Ruxton 2002, Dunbar 2003). Viewing individually distinctive patterns of interaction as attributes of sociality and analyzing these social attributes in conjunction with fitness measures across many species will allow us to gain further insights into long-standing behavioral questions.

Network analysis offers established methods for measuring social attributes defined from interactions among group members. Social network analysis has a long history of use in human sociological studies (Wasserman & Faust 1994, Scott 2000, Hanneman & Riddle 2005), and there has been a recent upsurge of interest in examining networks in many fields, most notably in physics (Strogatz 2001, Newman 2003b, Proulx et al. 2005, Boccaletti et al. 2006). Behavioral ecologists have also recognized the potential of this approach for studying animal groups (Krause et al. 2007, Croft et al. 2008, Wey et al. 2008, Sih et al. 2009). However, network analysis is still in its early stages in this field, and more tests are needed to establish its general utility for addressing behavioral ecology questions.

The main objective of this dissertation is to examine the biological causes and consequences of social attribute variation in a network context. I consider the theoretical basis for adapting network analysis to animal studies, then apply and test these methods in free-living mammals. In so doing, I aim to both contribute

further insights into the adaptive value of sociality and examine the general utility of animal social network analysis.

In Chapter 2, I review the basic theory and history of social network analysis and discuss its application in animal behavior. In Chapters 3 and 4, I apply some of the proposed measures and techniques from Chapter 2 to investigate the adaptive value of affiliative and agonistic interactions in yellow-bellied marmots. In Chapter 3, I examine the effects of age, sex, and kinship on individual attributes and the structuring of marmot social networks. In Chapter 4, I test hypotheses about the relationship between individual attributes and multiple fitness measures, and about how these relationships vary between different age-sex groups.

Chapters 2 and 3 were published in *Animal Behaviour* (Wey et al. 2008, Wey & Blumstein 2010) and are included in the published format with permissions from the journal. Chapter 4 was written for publication as a separate manuscript and is thus formatted for a targeted journal. All manuscripts were written with co-authors, and work was performed with the help of others. Chapters 2,3, and 4 are therefore written to reflect this.

STUDY SYSTEM AND GENERAL METHODS

Yellow-bellied marmots are large, hibernating ground squirrels found in sub-alpine regions throughout western North America (Armitage 2003). Field data for this

dissertation were collected from a population in and around the Rocky Mountain Biological Laboratory (RMBL) located in Gothic, CO (latitude: 38° 57' 29" N; longitude: 106° 59' 06" W), where the study colonies are distributed along a north-south elevational gradient in the East River Valley in Gunnison County. This particular population is part of long-term research, which has been continuous since 1962 (Armitage 1991, Schwartz et al. 1998, Ozgul et al. 2010). As part of ongoing work, marmots are regularly observed, live-trapped, and marked for individual identification. Observation and trapping data collected from 2003-2008 were used in this dissertation. Weather permitting, observations and trapping took place during mornings and afternoons, when marmots were most active (Armitage 1991), throughout the majority of their active season, which is approximately mid-April to mid-September at RMBL.

During observations, trained observers watched marmot colonies from a distance, so as not to influence behaviors, using spotting scopes and binoculars. We recorded all instances of behavioral interactions (i.e., all occurrence sampling—Martin & Bateson 1993). For each interaction, observers recorded the date, time, location, initiator ID, recipient ID, interaction type, and winner and loser IDs where appropriate. The ethogram of social behavior used was adapted from Johns & Armitage (1979) and Nowicki & Armitage (1979), and I further identified each interaction as affiliative (greet, allogroom, sit in contact, sit within 1 m, forage together, sniff anogenital region, play) or agonistic (aggression: bite,

box, chase, mount, mouth spar, pounce, push, snarl/hiss, wrestle; simple displacement, proximity displacement).

I then used these behavioral data to construct yearly affiliative and agonistic networks for four geographically distinct, permanent colonies: Bench-River, Marmot Meadow, Picnic, and Town. All network analysis was conducted in the program UCINET (Borgatti et al. 2006). All adults and yearlings observed more than 5 times that year were included in networks; pups born that year were excluded because they are not yet socially integrated into the colony. Data from observations and network analysis were used in Chapters 2, 3, and 4.

We live-trapped marmots using large metal Tomahawk™ traps baited with Omolene™ horse feed, and we marked and collected a suite of biological data and samples from each animal. Because of the intensive trapping regime, we catch virtually every mammal within the study area. Individual identification is crucial for network analysis, and marking methods included giving each marmot a set of metal ear tags with a unique number combination and a distinct dorsal mark with nontoxic black Nyanzol™ dye for identification during observations. In 2007 and 2008, we also combed marmots and counted fleas.

Whenever fecal samples were available in the trap and could be associated with an individual marmot, we collected them in plastic sealable bags. Fecal samples were immediately placed in coolers. At a lab in RMBL, 2 grams of feces were placed in formalin, and the rest was frozen at -20 degrees F. After transfer to

the University of California, Los Angeles (UCLA), we used OvaFloat™, a zinc sulfate, to perform fecal floats and detect presence of intestinal parasites from samples in formalin. Fecal glucocorticoid (stress hormone) metabolites were extracted from frozen feces at UCLA and sent to the University of Washington Center for Conservation Biology for radioimmunoassay. Data from these samples were used to determine the fitness measures used in Chapter 4.

ANIMAL SOCIAL NETWORKS

Social living often implies behavioral interactions and more complex social structure. While the consequences of group living and group size have been more extensively studied in a number of systems (Dunbar 1988, Hoogland 1995, Brown & Brown 1996, Krause & Ruxton 2002), the fitness effects of social interactions are less well understood. Interactions can have important effects and are important to study (Hinde 1976, Whitehead 2008), but most behavioral ecology studies do not explicitly measure them or only do so in very limited contexts. In social network analysis, social groups are modeled as interconnected units, and it is proposed that this approach will complement and extend past research on social structure, ultimately further our understanding of social complexity and the consequences of both direct and indirect interactions.

In Chapter 2, I suggest that applying network analysis to animal behavior can indeed advance the field by identifying and quantifying specific attributes of sociality, many of which are not captured by more common measures of sociality, such as group size. Sophisticated methods for network construction and analysis already exist in other fields but only recently have seen more interest and application in animal systems. However, careful consideration and more tests of theory are needed when adapting concepts from other fields to behavioral ecology. This chapter provides a prospective overview of social network analysis' general utility for the study of animal social behavior.

I first review basic network theory, present a brief history of social network analysis in human and animal systems, and go over some commonly used network measures. I then discuss possible issues that might arise from adapting network analysis to animal behavior studies and include results from an original study of the effect of sampling on network parameter estimates, which suggest that measures can be robust but that they should be used and interpreted with care. I end by highlighting promising directions for research in behavioral ecology. This chapter provides a prospective overview of social network analysis' general utility for the study of animal social behavior.

BIOLOGICAL CAUSES OF MARMOT NETWORK STRUCTURE

Individual characteristics can influence social structure in animal groups. Social behavior is likely to change with age, and it is important to understand observed outcomes within the context of life stages (Bekoff 1972, Hinde 1974, Chalmers 1983, Walters 1987). Developmental changes in social behavior can have important biological impacts, for instance on dispersal (Bekoff 1977, Holekamp 1984, Blumstein et al. 2009) and dominance (Bekoff 1974, Walters & Seyfarth 1987, Holekamp & Smale 1993, Hawley 1999). Social development may continue throughout adulthood (Bateson 1982, Mateo 2007), and it is important to consider context throughout an animal's life, especially in terms of long-term relationships and their effects (Connor et al. 2001, Payne 2003, Silk 2007).

Individuals may also choose to interact differently with others based on their characteristics, such as age, sex or kinship. Often individuals preferentially interact with others that are similar to themselves (in humans—McPherson et al. 2001, Newman 2003a; and in other animals—Lusseau & Newman 2004, Croft et al. 2005), and this may be a common influence on network structure.

Understanding processes of network formation can help us better understand basic issues in behavioral ecology, for example, the evolution of cooperation among unrelated individuals (Ohtsuki et al. 2006, Santos et al. 2006, Ryder et al. 2008).

In Chapter 3, I used social network attributes to examine biological correlates of individual social variation in free-living groups of yellow-bellied marmots. To measure social variation, I chose network measures that reflect an individual's tendency to initiate or receive both direct and indirect interactions. I asked how age, sex and kinship influenced patterns of affiliative (socially cohesive) and agonistic (socially competitive) interactions. Specifically, I predicted that individuals would vary in their tendency to initiate and receive interactions according to these characteristics, and that they would be more likely to interact affiliatively with more similar individuals and to interact agonistically with more dissimilar individuals.

I found that patterns of direct and indirect interactions changed significantly with age, with younger animals being more involved in affiliative interactions and older animals initiating more agonistic ones. Furthermore, in affiliative networks, marmots preferentially interacted with other individuals that were closer in age and more closely related. The results suggest that yearling yellow-bellied marmots are more important for maintaining social cohesion than has previously been recognized, and that marmot colonies are largely organized based on age group and kinship.

FITNESS CONSEQUENCES OF SOCIAL ATTRIBUTES

Social behavior consists of distinct and measurable social attributes, which have been measured in a variety of ways by behavioral ecologists (Hinde 1976, Dugatkin 1997, Krause & Ruxton 2002, Whitehead 2008). Attributes of sociality can have various associated fitness effects (Dewsbury 1982, Ellis 1995, Silk et al. 2003, Saplosky 2004, Cameron et al. 2009). A comprehensive attribute-based approach that examines the functional correlates of multiple separate attributes may offer more insight into the adaptive value of sociality, but this approach remains largely untested.

Attributes derived from social network analysis may be especially fruitful for this approach (Croft et al. 2008, Wey et al. 2008, Sih et al. 2009). To date, network attributes have been associated with fitness measures in multiple taxa, including reproductive success in birds (McDonald 2007, Ryder et al. 2009) and parasite infection in mammals (Corner et al. 2003, Madden et al. 2009) and lizards (Godfrey et al. 2009).

In Chapter 4, I tested hypotheses about the relationships between a number of social network attributes (Initiation, Reception, Out-closeness, In-closeness, Expansiveness, Attractiveness) in both affiliative and agonistic networks, and several fitness measures (annual reproductive success, parasite diversity, stress) in

four different yellow-bellied marmot age-sex groups (adult females, adult males, yearling females, yearling males).

Several general trends emerged. First, there were more benefits than costs associated with high values of social attributes. Sociality appears to be currently adaptive for this facultatively social species. Second, the particular association between social attributes and fitness measures varied between different age-sex groups, suggesting that the adaptive value of sociality differs for females and males and at different times of life. Third, absolute amounts of direct interaction consistently had more observable effects than indirect interactions or the relative amounts of direct interaction.

This study illustrated how an attribute-based approach can provide novel insights into the adaptive value of sociality. I suggest that certain types of social attributes will be particularly revealing in other species as well. Notably, these patterns only emerged by adopting an attribute-based approach, suggesting that partitioning sociality into a series of attributes may provide novel insights across social systems and species.

GENERAL CONCLUSIONS

In this dissertation I propose, test, and demonstrate the utility of social network attribute-based analyses for the advancement of behavioral studies. However, this

approach is still in its early stages, and my work suggests three potentially profitable directions for future research. First, more studies linking fitness consequences to social attributes are needed to gain a better overall picture of these associations in diverse taxa. At the moment, most studies are species-specific, and we lack the ability to say whether there are broad patterns or not. Second, real animal networks are dynamic, and current network models tend to be relatively static. There is now the computing power along with the interest in dynamic network modeling, and great strides are being made in this area. Linking dynamic computer models to processes in real biological systems is an important next step. Third, the social network approach lends itself to multiple levels of analysis, but so far most studies focus only on individual characteristics or group structure separately. Linking these two levels and exploring intermediate levels should emerge as an exciting challenge in current and future work.

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REVIEW

Social network analysis of animal behaviour: a promising tool for the study of sociality

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Social animals live and interact together, forming complex relationships and social structure. These relationships can have important fitness consequences, but most studies do not explicitly measure those relationships. An approach that explicitly measures relationships will further our understanding of social complexity and the consequences of both direct and indirect interactions. Social network analysis is the study of social groups as networks of nodes connected by social ties. This approach examines individuals and groups in the context of relationships between group members. Application of social network analysis to animal behaviour can advance the field by identifying and quantifying specific attributes of social relationships, many of which are not captured by more common measures of sociality, such as group size. Sophisticated methods for network construction and analysis exist in other fields, but until recently, have seen relatively little application to animal systems. We present a brief history of social network analysis, a description of basic concepts and previous applications to animal behaviour. We then highlight relevance and constraints of some network measures, including results from an original study of the effect of sampling on network parameter estimates, and we end with promising directions for research. By doing so, we provide a prospective overview of social network analysis' general utility for the study of animal social behaviour.

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Sociality implies a number of individuals living and/or interacting together, which can lead to complex social relationships and structure. Studying these aspects helps us understand the causes and consequences of sociality (Hinde 1976; Krause & Ruxton 2002; Whitehead 2008). Commonly used measures of social complexity (e.g. group size, mating system) have revealed many consequences of sociality (e.g. Côté & Poulin 1995; Hoogland 1995; Brown & Brown 1996; Dunbar 1998). Yet these measures only indirectly reflect the social relationships between individuals, and they assume homogeneity of effect on all individuals. We suggest that social network analysis will provide a deeper understanding of social complexity by measuring social

relationships directly. Formal network analyses will complement relationship-based approaches previously applied to animal behaviour (Hinde 1976; Whitehead 1997; Pepper et al. 1999). We believe that social network analysis has general relevance to all social systems, and that by expanding its application in animal behaviour, we will gain novel insights about the evolution and maintenance of sociality. In this review, we suggest how social network analysis can be used for studying animal systems, we use socially transmissible pathogens as a concrete example to illustrate specific points, and we identify possible constraints of this approach. Our goal is to briefly introduce and advocate the further use of social network analysis in animal behaviour; for an extensive review of this topic, see Croft et al. (2007).

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NETWORK THEORY

A network models a system composed of individual components (*nodes*) and their connections (*ties*; see Table 1

Table 1. Terminology**Basic terms**

Graph: a set of nodes and a set of relationships between the nodes, given by a matrix or visualized as a picture showing dots connected by lines

Node: a component of a network with known relationships to others in the graph model representing the network; in a social network, this can be an individual (person or animal) or group; also called a vertex or point

Path length: the shortest number of ties between two nodes

Sociomatrix: for a group with n members, an $n \times n$ matrix with each group member along the vertical and horizontal axes and each entry in the grid as the weight of the social relationship, if any, between the two intersecting individuals

Tie: a relationship between two components of a network, where the two related components are nodes in the graph model representing the network; in a social network, these can be any sort of social relationship, such as social interactions or information transfer; also called an edge or link

Individual (local) measures

Betweenness centrality: centrality based on the number of shortest paths between every pair of other group members on which the focal individual lies

Centrality: a measure of an individual's structural importance in a group based on its network position

Closeness centrality: centrality based on the shortest path length between a focal individual and all other members of the social group

Degree centrality: centrality based on the number of direct ties an individual has

Indegree (reception): the number of ties directed towards an animal, e.g. the number of social interactions it receives

Node degree: the number of ties a focal animal has; the number of other animals with which the focal individual interacts

Outdegree (emission): the number of ties originating from an animal, e.g. the number of social interactions it initiates

Intermediate measures

Clustering coefficient: the density of the subnetwork of a focal individual's neighbours; the number of ties between neighbours is divided by the maximal possible number of ties between them

Cliquishness: how much the network is divided into cohesive subgroups; a clique is a set of nodes where each node is directly tied to each other

Group measures

Average path length: the average of all path lengths between all pairs of nodes in the network

Density: the number of realized ties divided by the number of possible ties in the network

Diameter: the longest path length in the network

for definitions of italicized terms). The shortest number of ties between two nodes is the *path length* between that pair. This approach provides the best tools for understanding systems in which the most important characteristics are the connections between components. The social network approach addresses the structure of relationships and the mutual interplay between the individual and the group. While 'group' can be defined in many ways, here we use 'group' to mean the network as a whole, or the collection of potentially interacting individuals that are distinguished from other such collections of individuals. As with other definitions of 'group', this can theoretically range from two individuals to whole populations. For simplicity, here we generally refer to intermediately

sized groups, such as a herd of horses or a colony of birds. Two major reasons to use formal network analysis are that it provides formal descriptors (definitions and measures) for characterizing social groups and that, by providing quantitative measures of relationships, it allows us to test statistical models about relationships and structure (Wasserman & Faust 1994).

In social networks, nodes are social entities, which can be individuals or units (e.g. corporations in a business network), and ties are social relationships between two nodes at a given time; these can be interactions or associations (e.g. business dealings or friendships). In animals, relationships can include well-studied social interactions (e.g. agonistic interactions that create dominance hierarchies or grooming relationships in primate affiliative networks), as well as transmission events (e.g. pathogens, signals or social learning), resource sharing (e.g. food, territories or even heat in socially thermoregulating animals) and kinship ties. Ties can also have weight, direction and sign (i.e. positive or negative) to provide additional details about interactions (Fig. 1). In an unweighted (binary) network, all ties have value of 1, reflecting presence of a relationship between two nodes, and absence of a relationship is denoted by a 0. In a weighted network, ties reflect the strength of the relationships and can have different values. In a nondirected network, ties simply show that two nodes are connected. However, in a directed network, there can be potential inequality in the relationship, and A–B may not be the same as B–A. In animal behaviour, an easy way to conceptualize directionality is as directed social interactions, where ties reflect the initiator and recipient of the relationship (but note that directed ties need not have an initiator or recipient, e.g. A is the boss of B). Positive and negative values of ties can denote the nature of interactions or their effects on individuals. A network is commonly depicted visually as a *graph* (Fig. 1), also called a sociogram for social networks. More useful for quantitative analysis is a *sociomatrix* (a matrix with each node along the vertical and horizontal axes and each entry in the grid as the weight of the social relationship, if any, between the two intersecting nodes), and this form is the basis for many network analysis programs.

Hereafter, we use the term 'node' interchangeably with 'individual', and 'tie' with 'relationship'. While other terms have been used for these concepts, in animal social networks, we anticipate that nodes will most commonly represent individuals, and we choose 'relationship' rather than 'relation' (which is common in sociology) to avoid confusion with the term 'relatedness', which might limit the idea of social relationships. Here and elsewhere, we will illustrate the biological relevance of network concepts with the example of socially influenced transmission of a pathogen in a group of animals. Pathogen transmission can be influenced by social networks through rate of contact as well as overall social structure. While social influence can be general as in an airborne disease (e.g. a cold virus) that will be influenced by proximity and all types of social interactions, we will use the specific case of sexually transmitted diseases (STDs) and sexual networks. In this system, nodes are potentially sexually active

individuals, and ties are sexual relationships along which an STD may be transmitted. Binary ties would simply reflect the presence or absence of a sexual relationship, while weighted ties might reflect different rates of sexual contact between two individuals. Directed ties may become important if only one individual in a pair is infected, and the flow of the transmission can only go from one direction to another. While we use the example of disease, in which it may be desirable to minimize transmission, it is important to realize that in other cases (e.g. communication) selection should act to maximize transmission.

Broadly, the scope of network measures ranges from describing individuals to groups, with intermediate 'mesoscale' measures in between. At an individual level, network measures can describe the neighbourhood of a focal individual, patterns of direct and short indirect ties, and effects of strong and weak relationships. An example of an individual measure is *node degree*, which is the number of direct ties an individual has, i.e. the number of other individuals with which it has relationships. Direct ties are a focal individual's immediate connections; indirect ties are those with individuals more than one step away (see Fig. 2c). Although the relevance of indirect and weak interactions is not always obvious, their effects can be significant (see Granovetter 1973). For example, an individual's chance of contracting an STD depends not only on its own sexual partners, but also on their sexual partners. An infected individual may ultimately pass the disease to someone several partners removed, so an individual may be affected by anyone to whom it is connected through a continuous chain of intermediates. Thus, in addition to disease characteristics such as virulence, the nature and structure of social relationships will also affect likelihood and paths of transmission. In this way, social network analysis should explain biological phenomena that are influenced by indirect relationships better than other measures, such as group size, which do not contain sufficient details about individual social relationships. Importantly, network measures are calculated from explicit mathematical formulae, offering objective measures of individual and group sociality, and many measures can be standardized by dividing by group size, facilitating comparisons between groups. Thus, they may be useful for comparative studies (Faust & Skvoretz 2002; but see also Faust 2006 for issues that arise when comparing networks with very different sizes and densities).

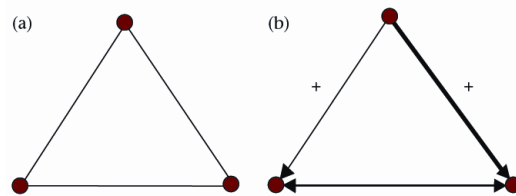


Figure 1. (a) A simple three-node network (triad) with ties that are unweighted, nondirected, and have no sign. (b) The same network with ties given weights, directions and signs, providing more information about the network; this triad also illustrates transitivity and a reciprocal negative relationship between the two bottom nodes.

At a group level, network measures can describe the overall structure and possible stability (or vulnerability) of groups. Examples of group measures include *average path length*, the average of all path length between all pairs of individuals in the network, and *diameter*, the longest path length in a network. In social networks, group-level stability has implications for the removal (death or emigration) or addition (birth or immigration) of individuals, and for the extent to which structure influences network function or efficiency. These properties can only be understood in a network context and at the level of the whole network, and thus modern network theory can be the basis for a more holistic understanding of how social interactions influence group structure and dynamics. In the case of an STD, some network structures may allow for faster or more pervasive spread of the disease, and some social groups may be more at risk than others (Klov Dahl et al. 1994).

PREVIOUS NETWORK STUDIES

Network theory originated in mathematical graph theory and was soon applied to other fields (e.g. sociology: Cartwright & Harary 1956; business: Levine 1972; markets: Burt 1988; political science: Harary 1959, 1961a; ecology: Harary 1961b). Social network analysis has a long history of application in human sociology (Wasserman & Faust 1994; Degenne & Forsé 1999; Hanneman & Riddle 2005; also see the scientific journals *Social Networks*, *Journal of Mathematical Sociology* and *Connections*), and some network phrases describing sociological phenomena are even in general usage, e.g. the idea of 'six degrees of separation' based on a study by Milgram (1967) and popularized in a play (Guare 1990) and movie (Guare 1993). Network concepts have also been topics of recent popular literature (Gladwell 2000; Barabási 2002; Watts 2003). In various fields, social network analysis has contributed novel insights through the relationship-based approach. In epidemiology, for example traditional models of disease transmission assume random interactions between individuals (Anderson & May 1991), but social relationships are not random and can strongly affect the spread of disease. These effects can be subtle, but still change disease transmission dynamics (Watts 1999). The utility of network models to incorporate patterns of social relationships is ideally illustrated in the case of an STD, whose transmission can only occur through the network of sexual relations and cannot be accurately modelled without understanding social structure (reviewed in Liljeros et al. 2003). Yet while network analyses became important tools in many fields, there was a limited and delayed application in ecosystems ecology (Levine 1980), in which it was mostly restricted to economic input–output analyses (Hannon 1973). Remarkably, there was even less application to behavioural sciences; ethologists mostly restricted network analyses to describing dominance relationships from observed agonistic interactions (e.g. Appleby 1983; Archie et al. 2006). Note, however, that concepts of dominance developed quite independently of social network analysis (e.g. de Vries et al. 2006).

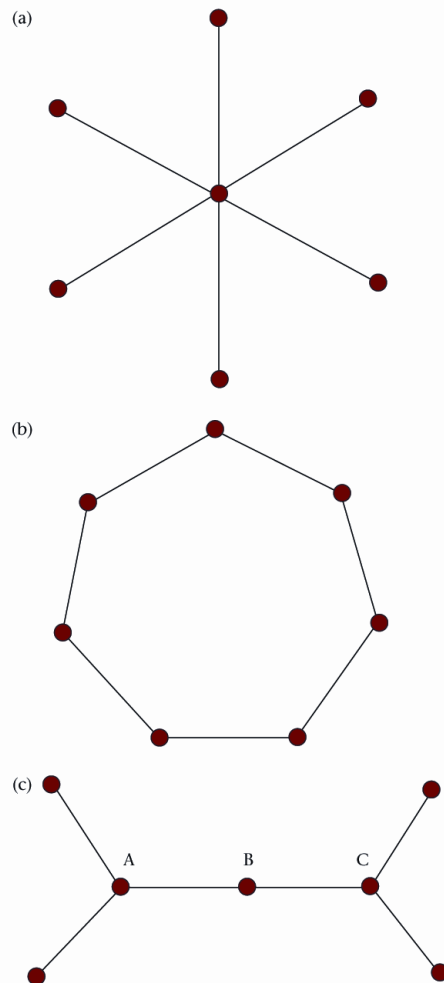


Figure 2. Three networks, each with seven nodes but different topologies: (a) a 'star' network where the individual in the middle has the highest degree, closeness and betweenness centrality and where the network has maximal centralization overall; (b) a 'closed' or 'circular' network where all individuals have equal degree, closeness and betweenness, while centralization is 0; and (c) a network where individuals A and C have highest degree, but individual B has highest closeness and betweenness. Note that A and C are indirectly tied to each other through their direct ties with B.

A recent explosion in computer processing power has created the ability to handle enormous databases and has revolutionized our understanding of larger and more complex networks describing real data (Strogatz 2001; Albert & Barabási 2002; Newman 2003b; Boccaletti et al. 2006). In general, we are no longer computationally limited by the number of nodes that can be studied, and researchers have begun to ask novel questions of phenomena as diverse as the Internet (Barabási et al. 2000), traffic

patterns (Fekete et al. 2006), neural networks (Freeman 2005), food webs (Solé & Montoya 2001; Luczkovich et al. 2003), gene and protein networks (Milo et al. 2002), terrorist networks (Krebs 2002) and publication networks (Newman 2003a). There are both striking similarities and differences between diverse networks, and social networks may have some distinct properties of their own (Newman & Park 2003). In all of these cases, the study of networks fundamentally enhances our understanding of how parts are connected as a whole.

While some early sociometric analyses were applied to primates (Sade & Dow 1994), behavioural biologists have only more recently recognized the potential of modern network tools to broader contexts (McMahon et al. 2001; Fewell 2003; Proulx et al. 2005). In the last few years, there have been novel and diverse applications of current network theory to nonhuman taxa, demonstrating its potential for animal behaviour (Croft et al. 2007). Seminal work in bottle-nosed dolphins (*Tursiops* spp.) revealed many notable relational aspects of their social structure. Dolphin social groups showed a 'scale-free' pattern (meaning that the degree distribution of the network follows a power law: Barabási & Albert 1999), giving it similar properties (such as robustness to the random removal of individuals) of other scale-free networks, like the Internet or molecular networks. However, unlike previously studied scale-free networks, it was also robust to the removal of key individuals (Lusseau 2003). As in humans, affiliation by sex and age were important in group formation in these animals (but interestingly, unlike humans, dolphins did not affiliate by degree), and a few individuals held structurally important positions in the social network (Lusseau & Newman 2004). Furthermore, dolphin networks had 'small-world characteristics', a combination of highly clustered subgroups and short average path lengths, which exists in many human social networks and may be very efficient for communication (Watts & Strogatz 1998), and their ties were based mainly on short-term associations, suggesting a fission–fusion society (Lusseau et al. 2006). These studies and others (e.g. Connor et al. 1998; Nanayakkara & Blumstein 2003; Whitehead et al. 2005) used SOCPROG (Whitehead 2006), a valuable program for describing animal social structure from observed associations.

Social network analysis has also been used to describe complex social structure in fish. Guppies, *Poecilia reticulata*, had small-world networks, and the network structure predicted patterns of cooperation (Croft et al. 2004, 2006). A comparison of social networks in guppies and three-spine stickleback, *Gasterosteus aculeatus*, found significant structure with 'social cliquishness' (Croft et al. 2005). Mechanisms proposed to explain the observed structure included association of similar-sized individuals, shoaling tendencies and repeated interactions between individuals, traits that satisfy certain prerequisites for the evolution of reciprocity and cooperation.

Innovative network studies in pigtailed macaques, *Macaca nemestrina*, examined the effect on network structure of removing key individuals (Flack et al. 2005, 2006), using both simulated and experimental removals resembling genetic knock-outs used to identify gene function.

Results indicated that key individuals can have disproportionately large effects on network stability and that predictions based on simulations may not accurately approximate real-life consequences, a fact that often is not fully appreciated in network models of ecological food webs (Jordán & Scheuring 2002; Eklöf & Ebenman 2006).

Spatial association networks also have consequences for social animals. Rhodes et al. (2006) found a scale-free network in the pattern of roosting tree usage by white-striped freetail bats, *Tadarida australis*. A single habitat tree was the hub of the network, where nodes were roosting habitat trees, and ties were individual bats' roost-switching events. The topology of this spatial network could have consequences on the social life and epidemiology of these animals, since individuals using different roosting trees spread over a large area could meet with surprising frequency at the central communal roosting tree.

These studies in diverse taxa show how modern social network analysis can contribute novel insights to animal behaviour and how these findings may influence applications of behavioural studies. A common theme is the importance of relational data for understanding overall structure and the roles of individuals within that structure. While these studies have made important headway, modern social network analysis of animal systems is only in its earliest stages. Comprehensive network studies on more animal systems over longer time periods will enhance our understanding of sociality and will allow novel analyses and comparisons. Future studies must go beyond simple network description and begin to relate network structure to biological and evolutionary consequences.

NETWORK MEASURES

In this section we present some common network measures and discuss biological relevance to animal social behaviour in the specific context of a STD. This is not intended as a comprehensive description of all useful methods but rather as general suggestions to facilitate further research. We provide conceptual rather than formal definitions to highlight potential biological significance and to avoid confusion in some terms, for which exact definitions vary by source. For detailed definitions, formulae and methodology, see Wasserman & Faust (1994), Borgatti et al. (2006b) and Croft et al. (2007).

Individual Measures

Recall, individual measures are calculated from a focal individual's neighbours (those that are directly linked in the network). This individually based, or ego-centric, viewpoint describes a specific individual's position in the network, and the potential effect it has on (and receives from) others. An individual measure can reflect relationships with just those directly connected to the focal individual, or also individuals indirectly connected to the focal individual, up to a given number of steps. Specifications are set based on applicability to the study.

We defined *node degree* above as the number of direct ties a focal individual has. A related idea in a weighted

network is relationship strength, which is the weight of the tie (Barthélemy et al. 2005). In our STD example, node degree might be the number of other animals with which the focal animal copulates, and relationship strength, the number of times the focal animals copulates with each. Total copulations (the sum of all the relationship strengths) might reflect differences in number of chances for an animal to be exposed to the STD. Although they reflect slightly different aspects of social relationships, both of these measures will affect an individual's risk of infection, but one may be more appropriate in a given context. For instance, node degree may be more relevant for spread of a highly infectious disease, while total relationship strength might be more relevant for a less virulent disease that requires repeated exposures for infection. In a directed network, *indegree* is the number of ties directed towards an animal (i.e. the number of relationships in which it is the receptor), and *outdegree* is the number of ties originating from an animal (i.e. the number of relationships in which it is the emitter). The difference between indegree and outdegree, which can be a positive or negative number, reflects the local component of sociometric 'net status' (sensu Harary 1959). Indegree might reflect how susceptible an uninfected animal is to infection, and outdegree might reflect how contagious an infected animal may be. These same ideas apply to other forms of transmission, such as the transmission of information contained in signals (McGregor 2005) and the spread of innovations (e.g. Swan et al. 1999; Perry & Manson 2003). One limitation of social network analysis in modelling dynamic processes such as transmission is that a network represents a structure at one point in time, while inferences about dynamics must be made over longer periods of time (see Issues In Applying Social Network Analysis).

Centrality is one way to quantify an individual's structural importance in a group (Freeman 1979; Friedkin 1991). There are three common ways to describe centrality. *Degree centrality* is based on the number of direct ties an animal has, i.e. the more others with which an animal has relationships, the more central it is. Therefore, an animal with more ties will have more influence on those around it and possibly on the whole network (cf. a network 'star', Fig. 2a). An animal with more sexual partners has more chance of catching an STD, and if infected, more importance in spreading it. *Closeness centrality* describes how well connected an animal is to all others in the network, based on the inverse of shortest path lengths between that animal and every other animal in the social network. This measure reflects both direct and indirect relationships. An animal that is not directly connected to every other group member could be indirectly connected through one, two, three or more others. Closeness centrality better reflects an individual's potential influence on the entire group and is particularly relevant if the number of transmission steps matters, e.g. in terms of time and how fast transmission can occur. High closeness centrality indicates an infected animal's potential to quickly spread a disease to the entire group, not just to immediate neighbours as with degree centrality. *Betweenness centrality* also incorporates indirect interactions, but it reflects the

number of shortest paths between every other pair of animals in the network on which a focal animal lies. Betweenness thus indicates how important an animal is as a point of social connection and transfer. To contain disease transmission, it may be most effective to focus treatments on individuals with high betweenness. Besides being important in transfer, animals with high betweenness are likely to be important for group stability, and their removal (by death or dispersal) may fragment the group into smaller subgroups (McComb et al. 2001; Lusseau & Newman 2004; Flack et al. 2006). These three centrality concepts reflect different aspects of sociality, and are sometimes, but not always, correlated (Fig. 2). Another measure of centrality is 'eigenvector centrality' (Bonacich 1987), which factors in the importance of neighbours in determining centrality and may be more appropriate for weighted networks and association data (Newman 2004).

Intermediate Measures

Some network measures identify the presence of subgroups in the network, reflecting the distribution of the ties (Fig. 3). We call these 'intermediate' measures because they describe the relationships beyond a single individual (however, note that in very large networks, they will still be relatively local descriptors). *Clustering coefficient* quantifies the density of relationships among a focal node's neighbours (excluding the focal individual). The number of existing ties between neighbours is divided by the maximal possible number of such ties (e.g. if an individual has four neighbours, these neighbours may have $(4 \times 3)/2 = 6$ relationships among themselves). Clustering coefficient describes how densely (or sparsely) the network is clustered around the focal individual. *Cliquishness* describes to what extent the network is divided into cohesive subgroups. A clique is a set of nodes where each node is directly tied to each other (Fig. 3b), but less strict conditions can be defined as well. (A similar concept of 'compartment' has been used extensively in ecology, e.g. Krause et al. 2003.) The existence of subgroups may affect network robustness to fragmentation. With strong subgrouping, a network may be more quickly fragmented by removing a single or few animals or ties (e.g. by blocking a communication pathway). Higher clustering or cliquishness could also mean that transmission (e.g. of disease) would be very fast and complete within a subgroup, but slower throughout the entire network because transmission events would tend to stay within a subgroup. This could be beneficial or detrimental, for instance, by reducing disease or information transfer.

Group Measures

Group measures (calculated from the set of individual measures or defined only at the network level) describe aspects of overall network structure. Importantly, they go beyond simple measures of group size or composition, which are independent of the network of relationships. Diameter, mentioned previously, is the longest path length in the network (so if the diameter is n , no two individuals

are more than n steps away from each other), and is a very basic measure of how well connected the network is. Generally, individuals in a group with a smaller diameter are connected to each other through fewer intermediates, and transfer between individuals is potentially faster than in a group with larger diameter. The average path length also gives a general idea of the network's overall connectedness, and a shorter average path length again suggests potential for quicker transfer among all group members.

Cohesion is defined in many ways, both colloquially and in the network literature, but generally, the term describes how well a group is connected based on more sophisticated calculations. One measure of cohesion is *density*, the number of ties present divided by the number of possible ties in the network. Density is generally calculated only for unweighted networks, and while some methods to measure density in weighted networks have been proposed (Wasserman & Faust 1994), they are not universally accepted, and we do not address them here. A group with higher density has more ties per individual than a group with lower density and therefore, is theoretically more cohesive. Another important concept is transitivity, which is the idea that if A has a relationship with B, and B has a relationship with C, then A has a relationship with C as well. Also important is the idea of reciprocity, which reflects how many of the relationships are mutual. Together, transitivity and reciprocity tell us more about how well balanced relationships are (Fig. 1b). For example, two groups could have the same density, but one could have higher reciprocity, indicating that the interactions are more balanced overall. Greater cohesion, transitivity and reciprocity might all suggest a greater potential for transmission within a network. With affiliative relationships, greater cohesion, transitivity and reciprocity might

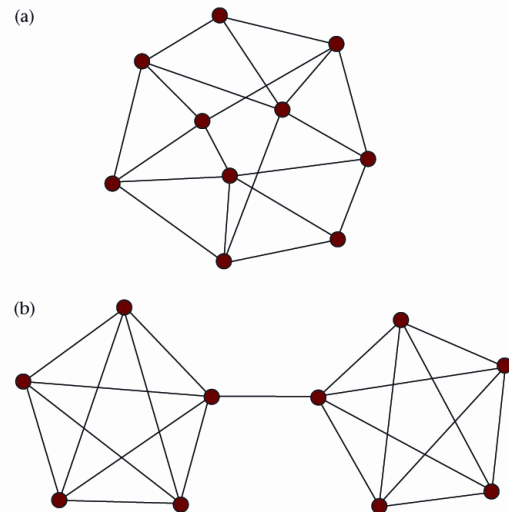


Figure 3. Two 10-node networks: (a) with no distinct subgroups, and (b) with two distinct subgroups (two cliques, i.e. groups of nodes with all possible ties among them, forming two complete subgraphs).

suggest a more tightly knit social group, in which positive interactions are consistent among triads and are mutual.

ISSUES WHEN APPLYING SOCIAL NETWORK ANALYSIS

Spatial and Temporal Limitations

Space constrains network structure, limiting the ways in which animals can construct their social networks and making some relationships and structures impossible or less likely than others. For example, locomotor ability, habitat topology and resource distribution will all influence the possible set of relationships. It is important to understand whether the observed social networks are distinct from relationships explained solely by shared space use (see Lusseau et al. 2006). Temporal limitations also arise because networks reflect the state of relationships in a group as if it were at one point in time, even if the data were collected over a longer period. Not all of the relationships represented may have existed at the same time, nor indeed may have all the individuals been together simultaneously. Network analysis assumes that the relationships included are relatively stable over time, and this assumption must be understood when using and interpreting networks. To examine network dynamics, one must look at how a network changes over time (e.g. by reconstructing and analysing the network at different points in time), or infer dynamics from the observed structure at only one point in time. One possible way to examine how temporal limitations may change network measures is to use permutation methods (Bejder et al. 1998; Whitehead 1999; Whitehead et al. 2005) to compare network measures calculated from permuted networks with measures calculated from the original networks.

Defining the Network

The decision about which individuals to include in a network analysis will affect the subsequent network structure and parameter estimates. Including too few individuals may give a truncated picture of the network, while including too many individuals may result in an unwieldy or highly fragmented network. In a fragmented network, the network is split into two or more unconnected subgroups, between which there are no interactions or communication. A number of network statistics cannot be defined and calculated for unconnected networks (e.g. diameter), while others generate misleading artefacts (Kossinets 2006). Thus, it is essential to carefully define a network in a way that reflects a biologically relevant level of resolution. For example, if the question is how social structure differs between populations of animals on isolated islands, it would be appropriate to define each island as a network, whether or not each is fragmented, in order to make comparisons between islands. However, if the question is how quickly information might be passed among connected individuals, then it would be inappropriate to look at a fragmented population (where, by definition, information cannot be

transmitted). In this case, one might use connected components (sets of individuals that can all be tied to each other, whether directly or through intermediates) as the unit of analysis.

Robustness of Parameter Estimates

All descriptions of sociality are generated by sampling behaviour, and sampling might affect our ability to estimate network parameters. Missing data can significantly alter network measures (Kossinets 2006), although centrality measures calculated from subsets of the data may retain their relative relationships to each other despite sometimes large absolute differences (Costenbader & Valente 2003). Removal trials on simulated data showed predictable trends in the response of centrality measures, suggesting that confidence intervals can be established (Borgatti et al. 2006a).

To examine how sampling affects real networks, we conducted a series of removal trials on data collected by observing social interactions in yellow-bellied marmots, *Marmota flaviventris*, a facultatively social, ground-dwelling, sciurid rodent. Marmots in and around the Rocky Mountain Biological Laboratory, Colorado, were individually marked and systematically observed for the occurrence and nature of all social interactions (see Blumstein et al. 2004 for methods). We tested the robustness of several network measures by calculating the network measures with the complete data set of all observed social interactions (we defined relationships as social interactions), followed by random removal of 10%, 20%, 30%, etc., up to 90% of the observations. Each removal trial was replicated 10 times, and the measures were recalculated for each subset. Our data were directed and weighted. We used analysis of variance (ANOVA) to determine what percentage of data removal resulted in a significant change in the network measure of interest. While these data are technically nonindependent, ANOVA is useful in a bootstrapping study such as this. The results of these removal trials for individual and group measures are presented in Tables 2 and 3. The standard error within each trial was low, indicating that, for a given sample size, network parameters were measured precisely.

Overall, many network measures were relatively robust to reduced sampling effort, suggesting that, in this system, we were sampling sufficiently to obtain representative network measures. In general, measures calculated only from direct interactions (e.g. degree centrality) were more sensitive to data removal than were measures calculated from indirect interactions (e.g. closeness and betweenness). However, measures incorporating indirect interactions also showed less consistent trends. This suggests that degree will steadily decrease as more and more interactions are removed, but changes in indirect interactions will be less predictable. Diameter was extremely robust, probably because it provides little detail about the relationships in the network as a whole and was calculated based on redundant paths (i.e. if there are multiple relationships between two individuals, removing all but one of those interactions will still make no difference in the diameter). Cohesion (calculated based on reciprocity) was also robust, although asymmetries tended

Table 2. The effect of randomly removing observations on estimates of individual network parameters

ID number	Outdegree: weighted	Indegree: weighted	Node degree: unweighted	Node degree: weighted	Closeness centrality	Betweenness centrality
1382–1397	30	30	50	30	70	90
4016–4070	0	0	60	0	60	80
4026–4050	0	0	70	0	60	60
4079–4033	20	20	60	20	90	80
4682–4698	0	20	50	0	60	90
4703–4002	0	0	70	0	90	60
4711–4706	20	20	60	30	60	90
4715–4716	20	0	70	0	60	50
4844–4853	0	20	70	0	90	80
Average	10%	12%	62%	9%	71%	76%

Marmot social groups were defined based on spatial overlap (see [Nanayakkara & Blumstein 2003](#)). Data are the percentage of the original data that could be removed randomly with no significant ($P > 0.05$) difference in the value of the network measure.

to be exaggerated with less data. Density was less robust to data removal because as the number of interactions decreased, the potential number of interactions did not, so this measure necessarily changed quickly with data removal.

Other Considerations

Using network measures in combination will develop a more comprehensive understanding of social relationships. For example, using individual, intermediate and group measures together will provide a broader view of overall social behaviour. The type of relationship data used should depend on the questions being asked and the biology of the system under study. For instance, focusing on grooming bouts is an appropriate way to study affiliative associations in primates ([Sade & Dow 1994](#); [Silk et al. 2003](#)), whereas agonistic interactions are used to examine dominance hierarchies ([Appleby 1983](#); [Archie et al. 2006](#)).

Whether weighted, directed, and signed data are used will also affect the measures calculated ([Vasas & Jordán 2006](#)). While weighted and directed information should give a more detailed picture of group structure and dynamics ([Newman 2004](#)), it may be more difficult to collect such data, and more detailed information may also be more sensitive to reduced sampling. If questions can be

answered just by the presence or absence of relationships, then binary data may be sufficient. However, weighted or directed information is indispensable if the question under study concerns the relative strength of relationships or the direction of transmission in the network.

Some network measures are calculated from shortest theoretical path lengths, but real transmission might not occur along these paths. Whether individuals perceive only their local neighbourhood or the entire network, along with the extent of an individual's control over transmission, can drastically change network dynamics. Given more knowledge about network structure, an individual might choose (or avoid) certain paths. In some animal groups, contact and transmission events may depend largely on chance. In these cases, it is unlikely for transmission to be along the most efficient path, and transmission may be more like diffusion. Additionally, the empirical effects of removing an important individual from a social group could be different from that predicted by simulated removals ([Flack et al. 2006](#)).

AREAS FOR FURTHER RESEARCH

Here we highlight some areas in which we feel social network analysis will bring immediate benefits (see also [Croft et al. 2007](#)).

Defining Social Groups

A nontrivial question is how to define a social group, and this will vary depending on the question. Social network analysis offers an alternate way to define animal social groups based on social relationships, rather than on spatial distribution or proximity. In nonhuman animals, especially those that are less social, it is also often difficult to distinguish between simple spatial and active social associations. [Lusseau et al. \(2006\)](#) showed that social relationships can be used to differentiate between the two, and groups defined by social relationships may be different from those based only on spatial proximity. Some recently developed methods are effective for picking out natural divisions or subgroups in networks ([Newman & Girvan 2004](#); [Newman 2006](#)).

Table 3. The effect of randomly removing observations on estimates of group-level network parameters

Group	Diameter	Density: unweighted	Density: weighted	Cohesion
BB	60	30	0	30
CC	80	0	0	20
CG	90	20	0	20
II	40	20	0	40
JJ	80	0	0	20
PP	80	20	0	30
Average	72%	15%	0%	27%

Marmot social groups were defined based on spatial overlap (see [Nanayakkara & Blumstein 2003](#)). Data are the percentage of the original data that could be removed randomly with no significant ($P > 0.05$) difference in the value of the network measure.

Identifying the Fitness Consequences of Sociality

Much is still not well understood about the fitness consequences of social relationships, and direct fitness correlates are rarely shown (but see [Silk et al. 2003](#)). In humans, the structure of an individual's social network can affect measures of health ([Berkman 1984](#); [Uchino et al. 1996](#); [Cattell 2001](#); [Friedman & Aral 2001](#)). Quantitative network measures can be correlated with fitness measures (e.g. reproductive success or parasites) to identify possible selective pressures acting on specific aspects of sociality. For example, if more socially central animals have significantly higher reproductive success, this would suggest a role of sociality in increasing fitness. Alternatively, an animal that has relationships with more different individuals could also have increased exposure to pathogens and might suffer higher risk of disease or parasites as a fitness cost. Social network analysis offers a way to re-examine fitness consequences and should contribute novel insights into the evolution and maintenance of sociality. Studying facultatively social species will be particularly important because they can illustrate how variable social traits are correlated with fitness trade-offs.

Identifying Important Individuals and Their Structural Roles

Group members may have different social roles or importance to the group ([McComb et al. 2001](#); [Lusseau & Newman 2004](#); [Flack et al. 2005, 2006](#)). Social network analysis offers quantitative measures of sociality that can be standardized for group size and possibly used to describe and compare social complexity of individuals and groups across different taxa. While there are issues with comparing networks of very different sizes ([Faust 2006](#)), we feel that this is still a useful starting point for comparison. Sociometric analysis can provide an objective, systematic way to determine dominance roles ([Archie et al. 2006](#)), and centrality measures can be used to identify important individuals in animal social groups ([Lusseau 2003](#)). In the case of wasp colonies, several centrality indexes have been tested for usefulness as predictors of queen choice, and results suggest that a directed meso-scale index is the best ([A. Bhadra, R. Gadagkar & F. Jordán](#), unpublished data). These measures provide different ways to define importance, and different measures may produce different rankings ([Jordán et al. 2006](#)). The most appropriate measure will likely depend on the question, but importantly, network measures provide a way to describe a continuum of social complexity that captures the social relationships within the group.

Developing a Comprehensive Understanding of Social Network Structure

Describing social networks in more species is essential for developing a comparative understanding of sociality and how it functions in different taxa, which will in turn allow us to better understand the evolution of sociality.

This requires more detailed and long-term data on social relationships, which may be difficult to obtain. However, some relational data exist (e.g. in many detailed studies of nonhuman primates) but have not been analysed in a network context, and it would be relatively easy to analyse already collected data sets. Types of relational data appropriate for network analysis include social interactions or associations.

Social insects are an ideal system in which to apply social network analysis ([Fewell 2003](#)), and some work on them is now underway. While classic studies showed that ant colonies may design their activity performance charts according to reliability theoretical principles ([Oster & Wilson 1978](#)), recent results show that network analysis is a more efficient approach to characterize and quantify the social behaviour (e.g. queen choice) of primitively eusocial tropical paper wasps and to better understand differences between closely related species ([A. Bhadra, R. Gadagkar & F. Jordán](#), unpublished data).

Other preliminary comparative results are also intriguing. [Faust & Skvoretz \(2002\)](#) found similarities in networks across very different species, while [Lusseau & Newman \(2004\)](#) found a distinct difference in assortativity between dolphin and human networks. There are also descriptions of the similarities and differences between social networks of two wasp species and students in classrooms ([A. Bhadra, R. Gadagkar & F. Jordán](#), unpublished data). These initial comparative studies show the wide applicability and promise of social network analysis for animal studies.

Identifying Key Characteristics of Stable Groups

Trait group selection models of social evolution focus on traits that are expressed at the group level ([Wilson 1975](#); [Wilson & Dugatkin 1997](#)). Social network analysis offers tools to identify group social traits, and so offers a way to gain novel insights into higher-level selection processes by identifying which network characteristics are important for group success. For instance, if groups with higher cohesion tended to out-produce or persist longer than groups with lower cohesion, it would suggest an important role for group cohesion in shaping the evolution of sociality. Used in conjunction with lagged association rates ([Whitehead 1995](#)) or other autoregressive methods to address temporal patterning ([Whitehead 1997](#)), social network analysis can be used to model group stability, but because models may not always accurately reflect empirical results, real tests of what group characteristics best promote stability will only come with more detailed longitudinal data.

Quantifying Anthropogenic Effects on Animals

Social network analysis could be helpful in wildlife conservation because it offers novel methods to document anthropogenic effects on animal social groups

(Tarlow & Blumstein 2007), and because it helps us better understand the mechanisms of disease transmission. Comparing animal social networks in disturbed and undisturbed areas could highlight changes in network structure that could have important fitness consequences. For some animals, disruptions in social structure may have negative effects in and of themselves (Flack et al. 2006) or lead to consequences for communication or mating, which can be better understood through social network analysis.

Understanding Disease Transmission in Natural Populations

There is an extensive literature on the application of networks to understand human epidemiology, making it a natural application to wildlife populations. The spread of different diseases may depend differentially on network structure because of varied modes of transmission (e.g. STDs versus nonsexually transmitted diseases: Altizer et al. 2003). As described above, social network analysis could help clarify to what degree the spread of various pathogens depends on social relationships in animals. Furthermore, identifying socially central animals could suggest which group members might be most influential in disease transfer. Some studies have already begun to apply network theory to better understand disease transmission in natural populations (Corner et al. 2003; Cross et al. 2004), and further research in this direction will be highly beneficial.

CONCLUSIONS

With this review, we hope to have illustrated the great potential that social network analysis has for the study of animal social behaviour. We expect that in the next decade there will be a fundamental increase in our understanding of social relationships and behaviour resulting from the wide-spread adoption of social network analyses, and we look forward to these insights.

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Social cohesion in yellow-bellied marmots is established through age and kin structuring

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Individual characteristics and choices can influence social structure in animal groups. Social behaviour is likely to change throughout an individual's life, resulting in different social roles at different ages. Individuals may also choose to interact differently with others based on their age, sex or kinship. We used social network analysis to examine biological correlates of individual social variation in free-living groups of yellow-bellied marmots, *Marmota flaviventris*. To measure social variation, we chose network measures that reflect an individual's tendency to initiate or receive both direct and indirect interactions. We asked how age, sex and kinship influenced patterns of affiliative (socially cohesive) and agonistic (socially competitive) interactions. Specifically, we predicted that individuals would vary in their tendency to initiate and receive interactions according to these characteristics, and that they would be more likely to interact affiliatively with more similar individuals and to interact agonistically with more dissimilar individuals. We found that patterns of direct and indirect interactions changed significantly with age, with younger animals being more involved in affiliative interactions and older animals initiating more agonistic ones. Furthermore, affiliative networks tended to be structured by age and kinship. Our results suggest that yearling yellow-bellied marmots are more important for maintaining social cohesion than has previously been recognized, and that marmot colonies are largely organized based on age group and kinship.

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Individual characteristics and choices can influence social structure in animal groups. Social behaviour changes with age, and animals can play different social roles throughout their life. Animals develop and maintain many relationships, including mother–infant, play, and adult social and sexual relationships. Each stage of social development may have important long-term effects, and understanding overall development is essential to understanding the full expression and consequences of social interactions (Bekoff 1972; Hinde 1974; Chalmers 1983; Walters 1987). Early interactions may influence dispersal decisions (Bekoff 1977; Holekamp 1984; Blumstein et al. 2009) or dominance (Bekoff 1974; Walters & Seyfarth 1987; Holekamp & Smale 1993; Hawley 1999). These ontogenetic patterns may further influence the evolution of social systems, such as dominance in primates (Pereira 1995). Dominance rank can significantly influence reproductive success (Ellis 1995; Frank et al. 1995). The quality of long-term affiliative bonds, which promote social

cohesion, can also determine lifetime reproductive success (Connor et al. 2001; Payne 2003; Silk 2007; Silk et al. 2009). Individuals of varying ages may occupy different 'ontogenetic niches', because of their different body sizes and needs (Werner & Gilliam 1984). Within social networks, individuals may occupy and construct different but interconnected 'social niches', with associated variation in quality of social resources based on interactions (Flack et al. 2006). By extension, individuals may occupy a series of social niches throughout development. Certain individuals may be especially important for maintaining group stability and structure (McComb et al. 2001; Flack et al. 2006), and their removal can have profound implications for conservation (McComb et al. 2001).

Development continues throughout a lifetime (Bateson 1982; Mateo 2007), and as animals face continuously changing selective pressures, they are likely to show changing patterns of interaction. This change may be associated with increasing age or size (female African elephants, *Loxodonta africana*: Archie et al. 2006; female mountain goats, *Oreamnos americanus*: Côté 2000; male long-tailed manakins, *Chiroxiphia linearis*: McDonald 1989), and have associated fitness consequences (mountain goats: Côté & Festa-Bianchet 2001; long-tailed manakins: McDonald 1989). Other changes may be less predictable. For example, in fission–fusion societies, many associations are temporary and show high turnover (chimpanzees,

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Pan troglodytes: Pepper et al. 1999; elephants, *Loxodonta* and *Elephas* spp.: Payne 2003; bottlenose dolphins, *Tursiops* spp.: Wells 2003; spotted hyaenas, *Crocuta crocuta*: Smith et al. 2007, 2008), while other associations are strong and can last for much of an individual's lifetime. The specific causes of change or stability may be based on differences in typical juvenile and adult behaviour or choices of social partner.

Social groups can be described as a network of individuals connected by interactions (Wasserman & Faust 1994), and formal network analysis may be applied to social groups to understand better their structure and function (Krause et al. 2007; Croft et al. 2008; Wey et al. 2008; Sih et al. 2009). Previous applications include studies of parasites (Corner et al. 2003; Cross et al. 2004; Naug 2008; Godfrey et al. 2009), emergent social structure (Lusseau et al. 2006; Rubenstein et al. 2007; Sundaresan et al. 2007), group stability (Flack et al. 2006; Williams & Lusseau 2006; Naug 2009), patterns of cooperation (Croft et al. 2006; Santos et al. 2006; Ryder et al. 2008), dispersal patterns (Blumstein et al. 2009), and even future reproductive fate (McDonald 2007; Ryder et al. 2008). Network analysis offers the advantage of having well-defined and established measures that capture aspects of network structure. Within a network, all interacting individuals are interconnected. Thus, indirect interactions in which a focal animal never directly takes part may still have important consequences. For instance, the likelihood of contracting a sexually transmitted disease depends not only on immediate partners, but also on the partners' other sexual interactions. Moreover, animals may construct 'social niches' within a network, and those that occupy particularly important positions may have disproportionate influence on network structure (Flack et al. 2006). Social network attributes may even be heritable, suggesting that effects extend across generations and influence the evolution of networks characteristics (Fowler et al. 2009).

Animals may interact differentially with others based on their characteristics. The tendency of individuals to form ties with more similar individuals, or homophily, is widespread in many human social networks (McPherson et al. 2001; Newman 2003). Although the patterns vary across contexts, networks are often structured based on similarity in age, sex or kinship. Homophily may also be common in animal systems (Lusseau & Newman 2004; Croft et al. 2005) and thus provide a possible mechanism of network formation. It may also have important consequences. Network analysis can help us model the evolution of cooperation among unrelated individuals (Ohtsuki et al. 2006; Santos et al. 2006; Ryder et al. 2008), and a preference for interacting with kin may be a first step towards kin selection.

We examined age-related patterns of affiliative (socially cohesive) and agonistic (socially competitive) behaviour in yellow-bellied marmots, *Marmota flaviventris*, a ground-dwelling sciurid rodent. We predicted that the tendency to initiate and receive interactions would change with age, that individuals would tend to interact affiliatively with other individuals of similar age, sex and kinship, and that they would tend to interact agonistically with more dissimilar individuals. We followed individually identified marmots from ages 1 to 6 years, a period which includes important life transitions from yearling to young adult to older adult, and we compared development in measures of both direct and indirect interactions.

METHODS

Study System

Yellow-bellied marmots are one of the more socially variable of the 14 marmot species (Barash 1989). Traditionally, they have been

described as harem polygynous, with adult females forming the backbone of social structure through recruitment of female offspring to build matriline (Armitage 1991). However, groups vary considerably in size and number of adult males, adult females and yearlings in a given colony (L. E. Olson & D. T. Blumstein, unpublished data). While numbers of each sex are even at birth, adult sex ratios are highly female biased because of higher male mortality (Armitage 1991). Yellow-bellied marmots become sexually mature when they are 2 years old, but many adults do not reproduce until they are older because of reproductive suppression (Armitage 1991; Oli & Armitage 2003). As yearlings, most males and about half of the females disperse from the natal colony (Armitage 1991), and this dispersal decision in females may be influenced by their affiliative interactions (Armitage 1986; Blumstein et al. 2009). The first few years of life therefore represent distinct transitional phases, from subadult to young subordinate adult to older and more dominant adult.

In some marmot species, individual distinctiveness of behavioural profiles seems to increase with age (Barash 1989; Armitage 1991), and there may be other age-specific patterns of social behaviour. Yearling yellow-bellied marmots frequently engage in play and initiate affiliative behaviours, but they rarely show agonistic behaviours (Armitage 1991). Rates of affiliative interactions are lower in adults in general, and play behaviour is almost never initiated (Nowicki & Armitage 1979). Previous research also suggests that affiliative and agonistic behaviours in this system are kin based (Armitage & Johns 1982; Armitage 1991).

Observations

Yellow-bellied marmots (hereafter, simply 'marmots') were studied from 2003 to 2008 under a research protocol (ARC No. 2001-191-01) approved by the University of California Los Angeles Animal Research Committee on 13 May 2002, and renewed annually. Animals were trapped under permits issued by the Colorado Division of Wildlife. Observers watched marmots from a distance, so as not stress animals or influence behaviour. We sterilized metal eartags used for permanent identification and used nontoxic Nyanzol-D (Albanil Dyestuff Corp., Jersey City, NJ, U.S.A.) to mark the dorsal pelage of animals for identification during observations. We attempted to handle marmots minimally during trapping procedures and released them immediately afterward at the site of capture.

We focused on four colony sites (Bench-River, Colony 1; Marmot Meadow, Colony 2; Picnic, Colony 3; Town, Colony 4) in and around the Rocky Mountain Biological Laboratory (38°57'29"N, 106°59'06"W, elevation ~2890 m) in Gunnison County, Colorado, U.S.A. We defined our colonies based on geographically distinct areas between which there are virtually no exchanges of individuals within a year, except through rare dispersal events. (In our data set, only two individuals moved from one study colony to another study colony in the same year, and we omitted these individuals from the statistics.) This population has been under long-term study, and we followed standing protocols for trapping and marking animals (see Armitage 1982 for details).

During the active season (mid-April to September, from emergence from hibernation to immergence), trained observers monitored each colony on most mornings (0700–1000 hours) and some afternoons (1600–1900 hours), the periods of peak marmot activity (Armitage 1962). Observers sat at a distance (20–150 m) that did not influence behaviour, and followed social interactions through binoculars and 15–45× spotting scopes. We used all-occurrence sampling of social interactions. For each interaction, we recorded the type and the initiator and recipient. We divided interaction types into affiliative and agonistic (for ethogram details see: Johns

& Armitage 1979; Nowicki & Armitage 1979). Affiliative interactions included greeting, allogrooming, sitting in close proximity and play behaviour. Agonistic interactions included overt aggression (biting, chasing, fighting) and displacements. We excluded interactions that we could not classify clearly as affiliative or agonistic.

Social Networks

We constructed social networks based on observations for each colony in each year, and for affiliative and agonistic interactions, separately. Networks are systems of units (nodes) connected to each other (by ties). In this study, nodes represent individual animals, and ties represent presence of social interaction between two animals. The ties were directed and valued, meaning that they had directionality and weights based on total number of interactions. Directed ties have an initiator and recipient, such that if A chooses to interact with B, it does not necessarily imply that B chooses to interact with A. Maintaining tie directionality was important because we predicted that patterns of initiation and reception would change differently. All networks were constructed in and analysed with UCINET 6 (Borgatti et al. 2006). We excluded pups (young of year) from analysis because they were born halfway through the season and had limited interaction with individuals other than their mother or littermates (personal observation).

Individuals that were seen fewer than five times in a season (transient animals) were not considered part of the social group and were excluded from subsequent analysis. Therefore, while our networks are necessarily a summary of interactions observed over a season and do not capture within-year dynamics, we believe that they accurately include the regular members of the colony. In addition, because of the regularity of observations and the relative stability of group membership within a year, we elected to include rare interactions as ties (but see Croft et al. 2008 for discussion of excluding rare interactions). We assumed that these rare events represented real interactions between regular colony members. This was especially relevant in the case of agonistic interactions, which were relatively infrequent overall, yet were likely to be important to the individuals involved. We made these decisions to exclude any interactions with animals 'just passing through', while including all interactions between regular members.

Development of Individual Social Attributes

For each individual in each year, we calculated the following network measures of individual social attributes: 'expansiveness', 'attractiveness', 'out-closeness' and 'in-closeness' (Table 1; see also Wasserman & Faust 1994 for further details on these measures).

Briefly, expansiveness and attractiveness reflect a node's tendency to initiate or receive ties from other nodes, relative to the tendencies of others in the network. The calculation of

expansiveness and attractiveness uses exponential random graph models (ERGM) or p^* models (Faust & Skvoretz 2002; Robins et al. 2007) to control for the overall network density (the number of interactions present relative to the number that could exist) and the overall reciprocity (tendency of interactions to be mutual: A interacted with B and vice versa). The calculation generates an alpha and beta value, which we refer to in the current study as expansiveness and attractiveness, respectively, as per some sociological literature (Skvoretz & Faust 1999). Expansiveness and attractiveness are based only on direct interactions, which are interactions in which an animal participates directly (not to be confused with directed ties, which refer to ties with initiator and recipient). These two measures provide basic measures of a node's importance at a localized level (i.e. only to the extent of the node's immediate neighbours).

Closeness centrality (Freeman 1979; Friedkin 1991) is a measure of a node's connectedness to all other nodes in the network based on shortest path lengths (also called geodesics), where path lengths are measured in terms of social connections between two nodes. Closeness centrality is often thought of as the potential of a node to reach (or be reached by) all other nodes in the network, and it is thus an indicator of influence. The calculation of closeness is based on both direct and indirect interactions. The most commonly used measure of closeness centrality is the reciprocal of the sum of the shortest path lengths between the focal node and all other nodes in the network. The shortest path length between A and B is 1 if they directly interact, 2 if they are most closely connected through one other individual, and so on. We used an alternate measure of closeness, which is the sum of the reciprocals of the shortest path lengths. By summing the reciprocals, the unconnected nodes contribute 0 to the overall closeness score, rather than rendering the closeness score infinite and undefined, as is the case in the most common version of closeness. In a directed network, paths must follow the direction of the ties, so out-closeness is the closeness of the node based only on shortest path lengths of ties originating from the node, and in-closeness is the closeness of the node based only on shortest path lengths of ties terminating at the node. Using standardized values for closeness may facilitate comparisons among networks of different sizes (Beauchamp 1965; Wasserman & Faust 1994), so we used standardized values for out- and in-closeness. For the version of closeness used in this study, the standardized values are the unstandardized values divided by the maximum possible closeness score that a node could have given the number of nodes in the network, expressed as a percentage.

We chose these four measures (Table 1) to generate two pairs of measures that reflected individual importance as an initiator and as a recipient of interactions in the network, but that differed in whether they were calculated based on direct ties only or on indirect ties. This allowed us to compare results for expansiveness and attractiveness to out-closeness and in-closeness. In some networks there were isolates (i.e. animals that were observed and trapped in a colony but that were not observed interacting with other animals), and these were excluded from analysis because expansiveness and attractiveness are undefined for isolated nodes. Our results therefore are only for animals observed to interact.

We used linear mixed effects models with a restricted maximum likelihood method to look for age-related change in each of the social attributes, while controlling for random effects of individual. Social attributes (expansiveness, attractiveness, out-closeness and in-closeness) were the dependent variables in separate models, and exact age was a covariate. We also included sex, year, colony, and the interaction sex*exact age. Marmots are sexually dimorphic, and previous studies suggest some sexual

Table 1
General definitions of network measures (individual social attributes)

Measure	Reflects a node's	Based on
Expansiveness	Tendency to initiate interactions relative to other nodes in the network	Direct interactions
Attractiveness	Tendency to receive interactions relative to other nodes in the network	Direct interactions
Out-closeness	Ability to reach all other nodes in the network through short path lengths	Direct and indirect interactions
In-closeness	Ability to be reached by all other nodes in the network through short path lengths	Direct and indirect interactions

differentiation in social behaviour (Armitage 1991). We included the year and colony as variables in case there were unexplained yearly or group effects, possibly due to environmental factors not accounted for in our study. We fitted separate models for affiliative and agonistic networks for each social attribute. All individuals of known age (from ages 1–6 years) from 2003–2008 were included in the analysis. The unit of analysis was an individual in a year. Statistics were calculated in SPSS 16.0 (SPSS 2007).

We expected the tendency of young marmots to interact affiliatively and not agonistically to be reflected in social attributes, demonstrated by a negative effect of age on affiliative social attributes and by a positive effect of age on agonistic social attributes. If both direct and indirect interactions changed with age, we expected to see a stronger effect for measures of direct interactions, which seem more likely to reflect an individual's own biological characteristics, rather than measures of both direct and indirect interactions, which depend on extended interactions of multiple other individuals.

Dyadic Age, Sex and Kin Structuring

We tested whether similarity in age, sex or relatedness was a significant predictor of network structure using a quadratic assignment procedure (QAP) regression in UCINET (Krackhardt 1988; Borgatti et al. 2006). The QAP is a special case of the Mantel test and allows a dependent relationship matrix (DM) to be regressed simultaneously against multiple independent matrices (IM) representing dyadic attribute relationships. After performing a standard multiple regression across the corresponding cells of the DM and IM, the procedure then randomly permutes the rows and columns of the DM and recomputes the regression, thereby generating a matrix-specific distribution against which the coefficients of the observed matrix can be compared to determine P values. In our case, the DMs were the networks of affiliative and agonistic interactions, and the IMs were matrices based on similarity in age, sex and relatedness.

We ran the procedure with 2000 permutations per DM. To construct matrices based on similarity in age, individual age attributes were converted into an $n \times n$ matrix, where n was the number of individuals in a network, so that each cell in the matrix represented a measure of similarity in age between the row and column individuals. In UCINET, this was achieved using the 'Data>Attribute to Matrix' function. We measured age in two ways and analysed each separately: exact age and age class (adult or yearling). For exact age, the cells represented the difference in age between the two individuals (smaller difference = greater similarity in age), whereas for age class, the cells represented same (1) or not same (0) age classes. Matrices for the attribute sex were constructed in a similar fashion, and cells also represented same or not same (1/0).

Relatedness was determined based on 12 previously developed microsatellite loci (L. E. Olson & D. T. Blumstein, unpublished data), with an average $\pm$ SE of 13.4 ± 1.21 alleles per locus (range 9–22), mean expected heterozygosity of 0.827 and mean polymorphic information content of 0.807. The microsatellite primers and DNA were amplified using polymerase chain reaction on a Peltier thermal cycler (MJ Research PTC-200) and genotyped on an ABI 3730 DNA capillary sequencer (Applied Biosystems, Inc. Foster City, CA, U.S.A.). Alleles were analysed using GeneMapper Version 3.0 software (Applied Biosystems). The program Kingroup 2.0 (Kononov et al. 2004) was used to calculate pairwise relatedness between all individuals present in a given year. Genetic similarity matrices were constructed from pairwise relatedness coefficients (higher r value = greater kinship).

We regressed networks simultaneously against three attribute matrices: age, sex and kinship. In UCINET, this was achieved using the 'Tools>Testing Hypotheses>Dyadic (QAP)>QAP Regression>Double Dekker Semi-Partialling MRQAP' function. In this case, the unit of analysis was the network (the colony-year). Again, we analysed affiliative and agonistic interactions separately, and we also ran two separate regressions for attribute matrices based on age class and exact age. QAP regression results would support the predicted affiliative homophily based on age, sex and kinship if the characteristics had a significant ($P < 0.05$) positive coefficient in affiliative networks. Results would support the prediction that animals would interact agonistically with less similar individuals if the characteristics had a significant ($P < 0.05$) negative coefficient in agonistic networks.

RESULTS

Results were based on 4947 h of observation on marmot colonies from 2003 to 2008. A total of 12 094 observed social interactions (9993 affiliative, 2101 agonistic) from 361 observed individuals (170 females, 191 males) were used to construct social networks. During these years, average $\pm$ SD colony size was 28.6 ± 13.4 (range 9–54). Figure 1 illustrates two representative marmot social networks, showing variation in size and structure.

Development of Individual Social Attributes

Major results for fixed factors are reported in Tables 2 and 3. Further details on full variable effects are given in the Appendix.

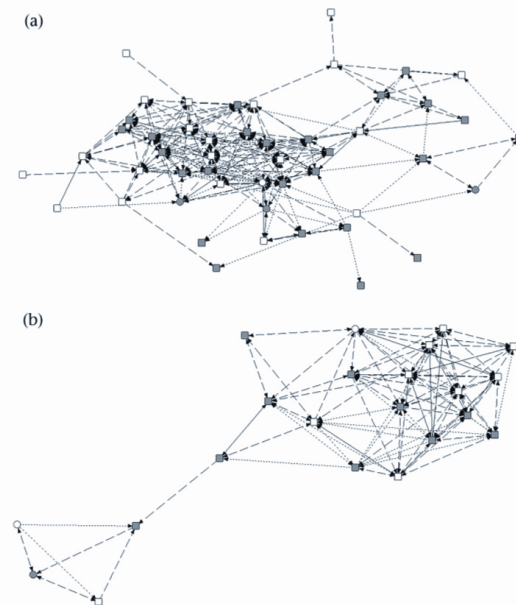


Figure 1. Two illustrative marmot social networks. (a) Picnic 2006. (b) Marmot Meadow 2007. These networks differ in size and structure. Circles: adults; squares: yearlings; grey nodes: females; white nodes: males; dashed lines: affiliative interactions; dotted lines: agonistic interactions; solid lines: affiliative and agonistic interactions; arrowheads (in black): direction of interactions (initiator to recipient).

Table 2
Tests of fixed effects for affiliative social attributes

Social attribute	Factor	Estimate	P
Expansiveness N=442	Intercept		0.993
	Year		0.931
	Colony		0.968
	Sex		0.702
	Exact age	0.061	0.768
	Sex*exact age		0.484
Attractiveness N=454	Intercept		0.001
	Year		0.996
	Colony		0.925
	Sex		0.379
	Exact age	−0.201	0.003
	Sex*exact age		0.619
Out-closeness N=442	Intercept		<0.001
	Year		0.924
	Colony		0.929
	Sex		0.070
	Exact age	0.491	0.688
	Sex*exact age		0.277
In-closeness N=454	Intercept		<0.001
	Year		0.001
	Colony		<0.001
	Sex		0.372
	Exact age	−2.640	0.002
	Sex*exact age		0.250

Factors marked in bold were significant at the 0.05 level. Estimates of effect are given for the covariate exact age. The full table for all parameter estimates is given in the Appendix, Table A1.

Tables A1 and A2. In affiliative networks (Table 2), attractiveness and in-closeness decreased with age (estimated fixed effect of exact age: attractiveness: -0.201 , $P = 0.003$; in-closeness: -2.640 , $P = 0.002$), but expansiveness and out-closeness did not change with age. Thus, younger animals received more affiliation through direct and indirect connections, but they did not initiate more. Year

and colony had significant effects on affiliative in-closeness (year: $P = 0.001$; colony: $P < 0.001$). No independent variables explained significant variation in expansiveness or out-closeness in affiliative networks, although there was a nonsignificant tendency for females to have higher out-closeness than males (estimated fixed effect of female: 5.143, $P = 0.070$), suggesting that females had farther-reaching indirect affiliative connections.

In agonistic networks (Table 3), expansiveness and out-closeness increased with age (estimated fixed effect of exact age: expansiveness: 0.594, $P < 0.001$; out-closeness: 3.903, $P < 0.001$), while attractiveness decreased with age (estimated fixed effect of exact age: -0.103 , $P = 0.010$). Thus, older animals initiated more direct and indirect agonistic interactions and received fewer direct ones. There was a significant interaction between sex and exact age for expansiveness ($P = 0.001$), suggesting that the increase in direct agonistic interactions initiated was stronger for males than females (see Appendix, Table A2). Year and colony had significant effects on agonistic out- and in-closeness ($P < 0.001$ for both).

Age, Sex and Kin Structuring

We summarize results for this section in the text and give full tables of results in the Appendix, Tables A3–A6. Across years and colonies, most affiliative networks were strongly kin structured, with more closely related individuals interacting more frequently (see Appendix, Tables A3, A4). This result was consistent whether similarity in age was measured by age class or by differences in exact age. In the former case, 19 of 24 networks had significant ($P < 0.05$) kin structuring, and three of the five nonsignificant networks showed positive trends ($P < 0.10$). In the latter case, 20 of 24 networks showed significant kin structuring, and two of the four nonsignificant networks showed positive trends. Affiliative networks also showed age homophily when similarity in age was measured by age class, but not when similarity was measured by difference in exact age. In the former case, 16 of 24 networks showed significant age structuring (although one of these showed the opposite trend from homophily), and two of the eight nonsignificant networks showed positive trends. In the latter case, only two of 24 networks were significant, and only one of the nonsignificant networks showed a marginal trend (negative coefficients in this case indicated homophily because smaller difference in age are interpreted as greater similarity). Overall, sex did not seem to play a large role in structuring affiliative networks, and in the few instances where it did, the coefficients showed both positive and negative effects.

In agonistic networks, we found no systematic effects of any attribute (Appendix, Tables A5, A6). There was significant kin structuring in fewer than half the networks, and in almost all cases, the pattern was in the opposite direction of what we predicted, with more closely related kin being more likely to interact agonistically. Age was a significant factor in even fewer agonistic networks and was also generally in the opposite direction of what was predicted, with more similarly aged individuals tending to have more agonistic interactions. Sex seemed to play little role in determining agonistic networks, but where it was significant, it seemed that animals were more likely to interact agonistically with the opposite sex.

DISCUSSION

Our results offer two main insights. First, we suggest that younger animals, particularly yearlings, are more important to marmot social cohesion than has been previously recognized. As primary receivers of affiliation, younger animals support social network cohesion, whereas the agonistic, competitive interactions

Table 3
Tests of fixed effects for agonistic social attributes

Social attribute	Factor	Estimate	P
Expansiveness N=276	Intercept		<0.001
	Year		0.786
	Colony		0.790
	Sex		0.181
	Exact age	0.594	<0.001
	Sex*exact age		0.001
Attractiveness N=376	Intercept		0.003
	Year		0.997
	Colony		0.988
	Sex		0.557
	Exact age	−0.103	0.010
	Sex*exact age		0.805
Out-closeness N=276	Intercept		<0.001
	Year		<0.001
	Colony		<0.001
	Sex		0.607
	Exact age	3.903	<0.001
	Sex*exact age		0.066
In-closeness N=376	Intercept		<0.001
	Year		<0.001
	Colony		<0.001
	Sex		0.949
	Exact age	−0.854	0.089
	Sex*exact age		0.740

Factors marked in bold were significant at the 0.05 level. Estimates of effect are given for the covariate exact age. The full table for all parameter estimates is given in the Appendix, Table A2.

initiated by adults would tend to decrease cohesion. It may be that affiliative interactions are not as important for older, more established adults (especially adult females, which remain in a colony for the rest of their lives) as they are for younger animals, which are socially subordinate and still face possible dispersal and integration into a new group. Our interpretation differs from the view of adult females as the foundation of marmot social structure, a view which is based on group membership across years rather than social interactions within a year (Armitage 1991). Our conclusion also differs from other social systems in which older individuals occupy more central cohesive roles, such as in African elephants (McComb et al. 2001). This distinction may reflect the difference between facultatively social marmots and more highly social species, which depend on social bonds *per se* for survival and reproductive success. It is possible that the quality of affiliative ties in marmots improves with age (as in humans: House et al. 1988), and thus adult females may be more important to social cohesion in this way. Testing this would require a different measure of relationship quality that was beyond the scope of our study. Our results are largely in keeping with observations that yearlings are more interactive overall and rarely engage in agonistic behaviour, but it was perhaps surprising that younger animals also lacked higher affiliative expansiveness scores. This probably stems from the measure of expansiveness, which controls for reciprocity of ties. Younger animals initiate a higher absolute number of interactions and have more social partners in affiliative networks (unpublished data), but it seems that many of these are reciprocated in response to received interactions, rather than independently initiated.

Our second major insight is that social cohesion, but not competition, is maintained through a preference for interacting with relatives of similar age. Thus, affiliative interactions are distributed unevenly, and this implies that colonies as a whole are not strongly cohesive. However, subgroups of closely related kin or same-age cohorts may be more strongly connected. Our results are similar to findings about age homophily in other systems (humans: McPherson et al. 2001; primates: Widdig et al. 2001; cetaceans: Lusseau & Newman 2004), but they differ subtly from previous findings on marmot age preference. Prior research found interage class interactions to be highly variable. Yearling females interacted affiliatively with both parents but agonistically with nonparent adult females, while yearling males interacted agonistically with most adults but sometimes interacted affiliatively with their mothers (Armitage 1974; Armitage & Johns 1982). In light of this, our results could reflect either active choice of affiliation within age class, or active avoidance of interaction with adults by yearlings, or both. Since marmots did not seem to discriminate based on similarity in exact age, it seems that the major social distinction is drawn between yearlings and adults, rather than between individuals of different absolute age.

The strong kin-biased affiliation we observed is consistent with other instances of kin preference in human (McPherson et al. 2001) and other social networks (e.g. Widdig et al. 2001), but contrasts with that in chimpanzees (Mitani et al. 2000) and long-tailed manakins (McDonald 2009). Previous marmot studies, in which relatedness was determined by observations alone, also found that female marmots directed more affiliation towards related females (Armitage 1991). We confirmed this result with molecular genetic data, larger sample sizes and network measures that accounted for possible network effects. Directing affiliative interactions preferentially towards kin might also indicate some degree of kin selection or the potential for it, although the presence of kin structuring in social networks may also result from factors other than kin selection, such as dispersal patterns (McDonald 2009). Female marmots recruit related females into their territory and

defend it against unrelated females, while males may tolerate related males on their territory (Armitage 1991; L. E. Olson & D. T. Blumstein, unpublished data). This result also suggests that stronger social bonds, which are more commonly associated with highly social species (cetaceans: Connor et al. 2001; primates: Silk 2007), may also be present to some degree in less social species among kin and age cohorts. Whether this kin preference arises through kin recognition specifically and what mechanisms drive the preference are questions requiring further study (Holmes & Mateo 2007).

Unlike affiliative networks, agonistic networks were less clearly structured, although there was a clear pattern of older animals initiating more and receiving fewer agonistic interactions. This pattern may result from larger size and greater competitive ability of older adults over 1- and 2-year-olds and also supports previous findings that older, dominant females reproductively suppress younger females. Contrary to expectations based on previous reports (Armitage 1991), we did not find agonism occurring more often between less closely related individuals or between different age groups. If anything, there was a slight tendency for more closely related individuals in the same-age group to interact agonistically. Perhaps this is a by-product of related females being found in closer proximity and yearlings being involved in so few agonistic interactions.

Considering the known sex differences and prior indications of behavioural dimorphism (Armitage 1991), we found fewer sex differences in network structure than expected. We found no main effects of sex, but the level of agonism initiated increased substantially more with age in males than in females, suggesting a stronger role of social competition in older adult males. Given our small sample sizes for adult males, it is possible that the conclusions we draw in this study give us limited general insight into these age–sex class and sex differences. Furthermore, males that disperse almost always do so beyond our study sites and therefore are not represented in our analyses. It is possible that adult males that dispersed showed different behaviour patterns than males that did not disperse; however, prior to dispersal, yearling males that subsequently disperse do not interact differently than yearling males that do not disperse (Blumstein et al. 2009).

The prediction that social attributes based only on direct interactions would show stronger age-related changes than social attributes that also measured indirect interactions was not upheld. Instead, the estimated effect of age on social attributes was always larger for out- and in-closeness than for expansiveness and attractiveness, indicating that age better explained variation in the two types of interactions combined. While there were significant effects of year and colony in some cases, these variables were included to control for environmental and other random variation not captured by our other variables, and therefore we can only suggest possible causes of the effects. Environmental conditions important to marmot biology, such as spring snowmelt, may explain widespread effects on all colonies. However, the years that showed significantly higher out- or in-closeness (2003, 2004, 2006) did not appear to have especially early or late snowmelt compared to other years. All four colonies varied widely in affiliative in-closeness scores, and Colony 2 (Marmot Meadow) had higher agonistic out- and in-closeness scores. Marmot Meadow is geographically small and has a relatively interactive group of marmots, but it is unclear why this would have an effect specific to agonistic networks. It seems possible that social conditions that could be characteristic of a site, such as population densities or group composition, might help explain the variation. The role of environmental conditions, both ecological and social, on network structure should be a productive direction for more research.

The current study also suggests some other directions for future work. We did not determine patterns of specific interactions (play,

aggression, etc.), and targeted data collection and analysis of specific interaction types could clarify patterns of affiliation and agonism in more detail. In the current study, separating interactions further would have made networks much sparser, especially agonistic ones, making it difficult to draw robust conclusions. There are also likely to be important within-year dynamics to be explored. Finally, the predictive power of social attributes at a young age for later consequences has so far received relatively little attention (but see McDonald 2007; Blumstein et al. 2009) and deserves further investigation.

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APPENDIX

Table A1

Estimates of fixed effects for individual affiliative social attributes

Social attribute	Parameter	Estimate	SE	P
Expansiveness N=442	Intercept	0.066	0.308	0.830
	Year=2003	0.043	0.234	0.855
	Year=2004	−0.160	0.215	0.457
	Year=2005	−0.125	0.204	0.540
	Year=2006	−0.137	0.205	0.515
	Year=2007	−0.075	0.195	0.699
	Year=2008	0.000		
	Colony 1	0.057	0.211	0.786
	Colony 2	0.056	0.226	0.804
	Colony 3	0.099	0.209	0.635
	Colony 4	0.000		
	Sex=female	−0.086	0.225	0.702
	Sex=male	0.000		
	Exact age	0.061	0.112	0.588
	Female*exact age	−0.085	0.121	0.484
	Male*exact age	0.000		
Attractiveness N=454	Intercept	0.393	0.284	0.167
	Year=2003	−0.068	0.212	0.750
	Year=2004	−0.015	0.204	0.942
	Year=2005	−0.050	0.188	0.792
	Year=2006	−0.065	0.191	0.732
	Year=2007	−0.077	0.182	0.674
	Year=2008	0.000		
	Colony 1	−0.114	0.196	0.561
	Colony 2	−0.125	0.209	0.551
	Colony 3	−0.071	0.193	0.712
	Colony 4	0.000		
	Sex=female	0.184	0.209	0.379
	Sex=male	0.000		
	Exact age	−0.201	0.105	0.057
	Female*exact age	0.057	0.114	0.619
	Male*exact age	0.000		
Out-closeness N=442	Intercept	21.424	3.781	<0.001
	Year=2003	0.351	2.885	0.903
	Year=2004	−0.920	2.727	0.736
	Year=2005	−0.291	2.550	0.909
	Year=2006	−0.159	2.624	0.952
	Year=2007	−2.214	2.521	0.380
	Year=2008	0.000		
	Colony 1	−0.817	2.417	0.735
	Colony 2	0.596	2.691	0.825
	Colony 3	−0.099	2.403	0.967
	Colony 4	0.000		
	Sex=female	5.143	2.829	0.070
	Sex=male	0.000		
	Exact age	−0.491	1.326	0.370
	Female*exact age	−1.579	1.453	0.277
	Male*exact age	0.000		
In-closeness N=454	Intercept	17.667	3.118	<0.001
	Year=2003	0.341	2.378	0.886
	Year=2004	3.059	2.248	0.174
	Year=2005	−2.478	2.210	0.239
	Year=2006	5.545	2.164	0.011
	Year=2007	−0.570	2.078	0.784
	Year=2008	0.000		
	Colony 1	6.443	1.993	0.001
	Colony 2	21.594	2.219	<0.001
	Colony 3	8.532	1.981	<0.001
	Colony 4	0.000		
	Sex=female	−2.083	2.332	0.372
	Sex=male	0.000		
	Exact age	−2.640	1.093	0.003
	Female*exact age	1.379	1.198	0.016
	Male*exact age	0.000		

Estimate = estimate of effect; Colony 1 = Bench-River; Colony 2 = Marmot Meadow; Colony 3 = Picnic; Colony 4 = Town.

Table A2
Estimates of fixed effects for individual agonistic social attributes

Social attribute	Parameter	Estimate	SE	P
Expansiveness N=276	Intercept	−1.055	0.323	0.001
	Year=2003	0.083	0.266	0.755
	Year=2004	0.171	0.233	0.464
	Year=2005	0.113	0.238	0.635
	Year=2006	−0.139	0.242	0.567
	Year=2007	−0.055	0.226	0.806
	Year=2008	0.000	0.000	
	Colony 1	0.098	0.218	0.653
	Colony 2	0.160	0.233	0.494
	Colony 3	−0.019	0.227	0.935
	Colony 4	0.000	0.000	
	Sex=female	−0.356	0.266	0.181
	Sex=male	0.000	0.000	
	Exact age	0.594	0.113	<0.001
	Female*exact age	−0.441	0.126	0.001
	Male*exact age	0.000	0.000	
Attractiveness N=376	Intercept	0.191	0.211	0.367
	Year=2003	−0.032	0.161	0.842
	Year=2004	0.015	0.146	0.938
	Year=2005	−0.035	0.145	0.810
	Year=2006	−0.025	0.142	0.860
	Year=2007	−0.053	0.136	0.696
	Year=2008	0.000	0.000	
	Colony 1	0.049	0.149	0.744
	Colony 2	0.031	0.159	0.844
	Colony 3	0.049	0.149	0.741
	Colony 4	0.000	0.000	
	Sex=female	0.092	0.156	0.557
	Sex=male	0.000	0.000	
	Exact age	−0.103	0.080	0.200
	Female*exact age	−0.022	0.087	0.805
	Male*exact age	0.000	0.000	
Out-closeness N=276	Intercept	−2.476	2.504	0.323
	Year=2003	5.114	1.910	0.008
	Year=2004	10.581	1.806	<0.001
	Year=2005	0.266	1.689	0.875
	Year=2006	2.802	1.738	0.107
	Year=2007	1.610	1.670	0.335
	Year=2008	0.000	0.000	
	Colony 1	2.888	1.601	0.072
	Colony 2	8.740	1.782	<0.001
	Colony 3	−0.498	1.591	0.066
	Colony 4	0.000	0.000	
	Sex=female	0.965	1.873	0.607
	Sex=male	0.000	0.000	
	Exact age	3.903	0.878	<0.001
	Female*exact age	−1.769	0.962	0.066
	Male*exact age	0.000	0.000	
In-closeness N=376	Intercept	8.033	2.140	<0.001
	Year=2003	3.838	1.633	0.019
	Year=2004	8.486	1.544	<0.001
	Year=2005	−1.645	1.443	0.255
	Year=2006	3.064	1.485	0.040
	Year=2007	1.380	1.427	0.334
	Year=2008	0.000	0.000	
	Colony 1	1.506	1.368	0.271
	Colony 2	6.928	1.523	<0.001
	Colony 3	−0.961	1.360	0.480
	Colony 4	0.000	0.000	
	Sex=female	−0.103	1.601	0.949
	Sex=male	0.000	0.000	
	Exact age	−0.854	0.750	0.256
	Female*exact age	0.273	0.822	0.740
	Male*exact age	0.000	0.000	

Estimate = estimate of effect; Colony 1 = Bench-River; Colony 2 = Marmot Meadow; Colony 3 = Picnic; Colony 4 = Town.

Table A3
QAP regression results for all colony-years in affiliative networks when similarity in age was measured by age class

Colony-year	Model P	Sex		Age		Relatedness	
		Coefficient	P	Coefficient	P	Coefficient	P
BR03	0.003	0.081	0.016	0.100	0.039	0.071	0.061
BR04	<0.001	−0.055	0.093	0.197	<0.001	0.237	<0.001
BR05	<0.001	−0.037	0.111	0.116	<0.001	0.121	<0.001
BR06	<0.001	−0.075	0.009	0.113	0.001	0.053	0.084
BR07	<0.001	−0.062	0.055	0.096	0.024	0.122	0.010
BR08	0.001	−0.063	0.066	0.030	0.301	0.135	0.003
MM03	0.002	0.096	0.210	0.305	<0.001	−0.036	0.393
MM04	0.006	0.059	0.212	0.130	0.072	0.124	0.046
MM05	0.003	−0.006	0.537	0.065	0.208	0.262	0.001
MM06	0.012	−0.131	0.025	0.116	0.049	0.265	0.010
MM07	<0.001	−0.03	0.233	0.164	0.001	0.203	<0.001
MM08	<0.001	0.016	0.339	0.234	<0.001	0.286	<0.001
P03	<0.001	−0.040	0.181	0.161	0.001	0.174	<0.001
P04	<0.001	0.050	0.099	0.104	0.003	0.100	0.008
P05	<0.001	0.004	0.400	0.095	<0.001	0.142	<0.001
P06	<0.001	0.009	0.349	0.113	<0.001	0.137	<0.001
P07	<0.001	−0.017	0.246	0.077	0.001	0.138	<0.001
P08	<0.001	0.018	0.307	0.006	0.417	0.256	<0.001
T03	0.057	−0.147	0.117	−0.001	0.485	0.158	0.130
T04	<0.001	0.055	0.154	0.219	0.004	0.310	0.003
T05	<0.001	0.043	0.182	0.119	0.064	0.206	0.004
T06	0.010	−0.039	0.308	0.027	0.384	0.178	0.006
T07	0.003	−0.019	0.444	−0.236	0.030	0.142	0.071
T08	0.004	−0.128	0.025	−0.086	0.207	0.228	0.017

Colony-year denotes a colony (Bench-River, Marmot Meadow, Picnic, Town) in a specific year (2003–2008). Coefficients and P values are presented for each variable (sex, age, relatedness) in separate columns. Effects marked in bold were significant at the 0.05 level.

Table A4
QAP regression results for all colony-years in affiliative networks when similarity in age was measured by difference in exact age

Colony-year	Model P	Sex		Age		Relatedness	
		Coefficient	P	Coefficient	P	Coefficient	P
BR03	0.003	0.082	0.011	−0.005	0.386	0.068	0.074
BR04	<0.001	−0.061	0.077	<−0.001	0.540	0.242	<0.001
BR05	<0.001	−0.016	0.325	−0.010	0.136	0.122	<0.001
BR06	0.004	−0.059	0.037	−0.020	0.201	0.076	0.022
BR07	0.002	−0.060	0.062	−0.017	0.188	0.147	0.002
BR08	0.001	−0.059	0.085	−0.026	0.262	0.140	0.003
MM03	0.196	0.063	0.236	−0.050	0.289	0.003	0.487
MM04	0.030	0.064	0.197	0.005	0.410	0.141	0.040
MM05	0.002	−0.009	0.489	<0.001	0.442	0.257	0.002
MM06	0.021	−0.128	0.030	0.002	0.420	0.234	0.014
MM07	<0.001	−0.026	0.285	−0.006	0.478	0.237	<0.001
MM08	<0.001	0.038	0.205	0.008	0.395	0.271	<0.001
P03	<0.001	−0.046	0.161	0.026	0.196	0.182	<0.001
P04	0.001	0.084	0.014	0.003	0.419	0.094	0.008
P05	<0.001	0.010	0.306	−0.007	0.367	0.150	<0.001
P06	<0.001	0.024	0.162	0.009	0.213	0.151	<0.001
P07	<0.001	−0.006	0.433	−0.010	0.257	0.142	<0.001
P08	<0.001	0.018	0.310	−0.038	0.042	0.256	<0.001
T03	0.061	−0.147	0.094	−0.060	0.337	0.158	0.097
T04	0.001	0.047	0.190	0.015	0.313	0.327	0.001
T05	0.002	0.039	0.207	<0.001	0.530	0.216	0.003
T06	0.010	−0.037	0.313	−0.008	0.311	0.175	0.008
T07	0.076	−0.018	0.445	−0.047	0.093	0.135	0.105
T08	<0.001	−0.125	0.021	−0.178	0.023	0.241	0.021

Colony-year denotes a colony (Bench-River, Marmot Meadow, Picnic, Town) in a specific year (2003–2008). Coefficients and P values are presented for each variable (sex, age, relatedness) in separate columns. Effects marked in bold were significant at the 0.05 level.

Table A5

QAP regression results for all colony-years in agonistic networks when similarity in age was measured by age class

Colony-year	Model	Sex		Age		Relatedness	
		P	Coefficient	P	Coefficient	P	Coefficient
BR03	0.004	0.064	0.031	0.083	0.064	0.050	0.134
BR04	<0.001	−0.094	0.004	0.074	0.017	0.098	0.010
BR05	<0.001	−0.001	0.490	0.028	0.110	0.082	<0.001
BR06	<0.001	−0.039	0.134	0.089	0.011	0.068	0.049
BR07	<0.001	−0.065	0.042	−0.019	0.315	0.127	0.003
BR08	0.006	−0.082	0.018	−0.018	0.332	0.051	0.116
MM03	0.005	0.140	0.086	−0.133	0.083	0.013	0.469
MM04	0.015	−0.046	0.190	−0.073	0.093	−0.090	0.076
MM05	0.025	−0.083	0.054	−0.052	0.206	0.009	0.424
MM06	<0.001	−0.041	0.324	0.157	0.009	0.346	0.002
MM07	0.016	0.010	0.375	−0.080	0.033	0.070	0.063
MM08	0.001	−0.033	0.176	−0.059	0.048	0.108	0.019
P03	0.017	0.010	0.382	0.028	0.180	0.069	0.019
P04	0.139	0.025	0.256	0.020	0.312	0.013	0.346
P05	<0.001	−0.014	0.250	0.059	0.003	0.036	0.053
P06	0.002	−0.034	0.043	0.043	0.023	0.022	0.154
P07	0.016	−0.018	0.167	0.044	0.020	−0.012	0.284
P08	0.001	−0.117	0.001	0.048	0.142	0.004	0.413
T03	0.010	0.112	0.283	0.202	0.099	0.329	0.034
T04	0.003	−0.019	0.369	0.117	0.034	0.284	0.006
T05	0.028	−0.060	0.087	0.016	0.349	0.082	0.076
T06	0.042	−0.022	0.404	0.044	0.297	0.120	0.054
T07	0.018	−0.086	0.112	−0.132	0.103	0.096	0.113
T08	0.002	−0.157	0.013	−0.122	0.115	0.061	0.213

Colony-year denotes a colony (Bench-River, Marmot Meadow, Picnic, Town) in a specific year (2003–2008). Coefficients and *P* are presented for each variable (sex, age, relatedness) in separate columns. Effects marked in bold were significant at the 0.05 level.

Table A6

QAP regression results for all colony-years in agonistic networks when similarity in age was measured by difference in exact age

Colony-year	Model	Sex		Age		Relatedness	
		P	Coefficient	P	Coefficient	P	Coefficient
BR03	0.011	0.065	0.023	0.025	0.141	0.048	0.140
BR04	0.001	−0.096	0.004	0.006	0.368	0.100	0.008
BR05	<0.001	0.004	0.437	0.012	0.206	0.082	<0.001
BR06	0.008	−0.026	0.237	0.033	0.128	0.086	0.018
BR07	0.001	−0.066	0.053	0.053	0.033	0.122	0.001
BR08	0.001	−0.085	0.010	0.016	0.325	0.048	0.117
MM03	0.006	0.154	0.064	0.334	0.019	−0.004	0.468
MM04	0.025	−0.048	0.199	0.131	0.057	−0.099	0.050
MM05	0.039	−0.081	0.062	0.054	0.191	0.012	0.417
MM06	<0.001	−0.038	0.351	0.219	0.001	0.304	0.002
MM07	0.048	0.008	0.381	0.070	0.098	0.053	0.140
MM08	0.001	−0.039	0.146	0.177	0.027	0.112	0.009
P03	0.024	0.009	0.391	0.068	0.076	0.071	0.016
P04	0.003	0.032	0.187	0.094	0.004	0.012	0.360
P05	0.023	−0.01	0.287	0.006	0.362	0.042	0.039
P06	0.025	−0.029	0.074	0.066	0.052	0.027	0.097
P07	0.127	−0.012	0.288	0.043	0.135	−0.010	0.339
P08	0.001	−0.119	0.002	0.001	0.483	0.006	0.406
T03	0.001	0.089	0.399	0.074	0.147	0.302	0.029
T04	0.006	−0.024	0.336	0.046	0.195	0.293	0.006
T05	0.001	−0.060	0.069	0.149	0.008	0.083	0.075
T06	0.057	−0.019	0.430	0.009	0.377	0.115	0.060
T07	0.035	−0.085	0.102	0.089	0.122	0.092	0.136
T08	0.016	−0.152	0.018	<−0.001	0.506	0.081	0.171

Colony-year denotes a colony (Bench-River, Marmot Meadow, Picnic, Town) in a specific year (2003–2008). Coefficients and *P* values are presented for each variable (sex, age, relatedness) in separate columns. Effects marked in bold were significant at the 0.05 level.

CHAPTER 4

A SOCIAL ATTRIBUTE-BASED APPROACH GENERATES NOVEL INSIGHTS ABOUT THE ADAPTIVE VALUE OF SOCIALITY

ABSTRACT

Social behavior consists of distinct and measurable social attributes. While many previous studies have categorized species as social or not, or quantified group size, studying the functional correlates of separate attributes may offer more specific insights into the adaptive value of sociality, but this approach remains largely untested. In a study of yellow-bellied marmots (*Marmota flaviventris*), we examined the relationships among a number of social network attributes (Initiation, Reception, Out-closeness, In-closeness, Expansiveness, Attractiveness) in both affiliative and agonistic networks, and several fitness measures (annual reproductive success, parasite diversity, stress) in four different age-sex groups (adult females, adult males, yearling females, yearling males). Several general trends emerged. There were more benefits than costs associated with high values of both affiliative and agonistic social attributes; thus, sociality appears to be currently adaptive for this facultatively social species. Additionally, the particular associations among social attributes and fitness measures varied among different age-sex groups, suggesting that the adaptive value of sociality differs for females

and males and at different times of life. Furthermore, absolute amounts of direct interaction consistently had more observable effects than indirect interactions or the relative amounts of direct interaction. This may be a general trend in animal social networks, but remains to be tested in other species. Notably, these patterns only emerged by adopting an attribute-based approach, suggesting that partitioning sociality and fitness measures into a series of attributes may provide novel insights in other species.

INTRODUCTION

Despite decades of study, much remains to be understood about the adaptive value of sociality. By living with others, animals may acquire a variety of benefits, but there are also emergent costs (Alexander 1974, Krause & Ruxton 2002).

Behavioral ecologists interested in the adaptive value of sociality have examined a variety of distinct social attributes and dimensions (e.g., whether or not animals live in groups, the size of groups they live in—Krause & Ruxton 2002; whether or not and how individuals may cooperate—Dugatkin 1997; and the social structure of individuals in groups—Hinde 1976, Whitehead 2008), but most often studies limit themselves to a subset of very basic measures, such as group living or group size. A shortcoming of this approach is that different social attributes may themselves have different costs and benefits. For example, if the number of

parasites to which individuals are exposed increases with group size (Côté & Poulin 1995), we may ask if this results solely from increased spatial proximity and overlap, or if the nature and types of social interactions are important. Distinguishing the relative effects of each social attribute requires measuring multiple attributes of sociality.

Specifically, if we decompose an individual's social behavior into discrete measures, we can ask which particular aspects of social interactions have adaptive value. This is particularly important because the same individual can be involved in multiple types and patterns of behaviors, which are likely to have different effects. For example, the outcomes of competitive dominance interactions are often associated, both positively and negatively, with stress and health in humans and other animals (Sapolsky 2004), and they may have fitness consequences (e.g., in spotted hyenas, *Crocuta crocuta*—Frank 1986, Holekamp et al. 1996; in primates—Walters & Seyfarth 1987; and across diverse taxa—Dewsbury 1982, Ellis 1995). On the other hand, socially cohesive behaviors, such as cooperation (Dugatkin 1997, Nowak 2006) also have obvious fitness consequences. Stronger affiliative social bonds increase lifetime reproductive success in female baboons (*Papio cynocephalus ursinus*, Silk et al. 2003, 2009) and female horses (*Equus caballus*, Cameron et al. 2009). Social systems are often structured by both affiliative and agonistic interactions, and without decomposing overall social behavior into discrete attributes, we cannot determine the explicit source of fitness

outcomes. We suggest that an attribute-based approach incorporating multiple social attributes will address this issue.

One way to measure discrete social attributes is with social network analysis, a technique that has received much recent interest for studying the structure and function of animal groups (Croft et al. 2008, Wey et al. 2008, Sih et al. 2009). Viewing social groups as networks of interconnected nodes focuses our attention on the connections among individuals. For example, if the spread of disease or information is influenced by social interactions, then the pattern of connections will play a major role in who gets infected or receives information and how quickly. Additionally, a network approach highlights the possible importance of direct interactions as well as indirect interactions among individuals connected through other network members. Indirect interactions can also have significant consequences because an individual's chance of contracting a disease or receiving information will likely depend on its social partners' connections as well. Importantly, network analysis offers precisely defined social measures based on the pattern of connections.

To date, most studies of animal social networks have been descriptive, but several recent studies show that network attributes can have fitness consequences. For instance, social attributes in male affiliation networks are associated with male reproductive success in two species of manakins: wire-tailed manakins, *Pipra filicauda* (Ryder et al. 2009) and long-tailed manakins, *Chiroxiphia linearis*

(McDonald 2007). Social attributes of spatial networks (burrow or crevice sharing) are also related to endoparasite infection in brushtail possums, *Trichosurus vulpecula* (Corner et al. 2003), and ectoparasite infection in the gidgee skinks, *Egernia stokesii* (Godfrey et al. 2009). Notably, Corner et al. (2003) also found that network attributes, which incorporated more complex patterns of interaction, were more precise and offered greater comparative utility than simpler social measures. Studying meerkats (*Suricata suricatta*), Madden et al. (2009) found that average ectoparasite loads influenced the structure of allogrooming and dominance networks.

A network attribute-based approach should provide a broad and flexible framework within which to study costs and benefits of sociality. However, the actual utility of this approach remains untested. We tested the general utility of an attribute-based approach for understanding the adaptive basis of sociality by applying it to free-living yellow-bellied marmots (*Marmota flaviventris*). We used six years of data to test the relationships among multiple fitness measures and multiple social attributes in both affiliative and agonistic networks. Moreover, we explicitly studied whether these network-derived attributes explained more variation than group size, a measure that has been used extensively in studies of animal sociality (Dunbar 1988, Hoogland 1995, Brown & Brown 1996, Krause & Ruxton 2002).

Hypotheses

We expected relationships among social attributes and fitness correlates to vary based on the nature of each, and in many cases based on the age and sex of marmots as well. Below, we develop a set of a priori expectations about putative fitness relationships.

Annual Reproductive Success: Social Cohesion and Competition

We expected the relationship between the number of offspring produced in a year and social attributes to differ between adult females and males, and we expected affiliative and agonistic attributes would have different effects. Across species, both competition and cohesion can influence reproductive success (competition—Dewsbury 1982, Ellis 1995; cohesion—Cameron et al. 2009, Silk et al. 2009). In yellow-bellied marmots, social factors influence reproductive success in both females and males, with maternal recruitment of female offspring into natal colonies being an important female reproductive strategy (Armitage 1991a). However, dominance rank is associated with male, but not female, reproductive success (Huang et al. 2011). Thus we expected both cohesion and competition would be associated with reproductive success in females and male, where affiliative and agonistic social attributes represent aspects of cohesion and competition, respectively, but that cohesion would be more prominent in female annual reproductive success and competition more prominent in males.

High values for affiliative attributes associated with more offspring would provide support for the cohesion hypothesis. Positive associations of some but not all attributes would distinguish those aspects of cohesion that specifically contribute to reproductive success. Increased annual reproductive success in larger social groups would also support the cohesion hypothesis. Though not expected, it is also possible that high values of affiliative social attributes to be negatively related to reproductive success. This would be contrary to the cohesion hypothesis and might suggest trade-offs between involvement in affiliation and offspring production.

Support for a role of competition in reproductive success would be seen if high values for attributes associated with initiating agonism were associated with higher reproductive success, and if high values of attributes associated with receiving agonism were associated with lower reproductive success. It is also possible that there are energetic costs to initiating agonistic interactions (Riechert 1988, Marler & Moore 1989, Valero et al. 2005), in which case, we might see negative relationships among the number of offspring and high agonistic initiation. A negative relationship between social group size and annual reproductive success would also be consistent with the competition hypothesis. Though not predicted, positive relationships among the number of offspring and high agonistic reception might represent an unexpected condition where animals that get “picked on” had more offspring.

Parasites

Parasites often constitute a cost of sociality (Alexander 1974, Krause & Ruxton 2002, Altizer et al. 2003, Nunn & Altizer 2006), and infection by contagious parasites generally increases with group size (Côté & Poulin 1995, Nunn & Altizer 2006). An underlying assumption is that increased social contact contributes to increased chance of infection (Anderson & May 1991), though it is difficult to distinguish the effects of increased social contact and host density (Altizer et al. 2003). Animals may also be able to counteract effects of increased exposure and reduce levels of parasitism through allogrooming, or other forms of behavioral compensation (Moore 2002, Altizer et al. 2003, Bordes et al. 2007). In the context of individual social attributes, high attribute values may be associated with higher (parasites as cost hypothesis) or lower (behavioral compensation hypothesis) parasite levels. We expect no significant differences in the relationships among social attributes and parasites based on age and sex.

To be consistent with the cost hypothesis, being better connected should be associated with having more parasites; we expect that high attribute values would be associated with higher levels of parasitism for both ecto- and endoparasites. Because all interactions increase physical contact or proximity, increasing the likelihood of infection, there should be no difference between effects of affiliative and agonistic interactions, or between interactions originating from or terminating

at an individual. We would also expect social group size to be positively associated with number of parasites.

To be consistent with the social compensation hypothesis, social attributes should be negatively associated with ectoparasites. Marmots may reduce the number of fleas on social partners by allogrooming, which is an affiliative interaction. Therefore, received affiliation should be negatively associated with the number of ectoparasites. Because the endoparasites examined in this study are fecal-orally transmitted, increased allogrooming would not be expected to reduce presence of intestinal parasites. In this case, we would also expect social group size to be negatively related to number of parasites because there would be more possible allogrooming partners available.

Stress

Social factors can both increase and alleviate stress in various species (De Vries et al. 2003). In yellow-bellied marmots, plasma glucocorticoid levels are influenced by the interactions among social factors and behavioral phenotypes (Armitage 1991b). We test for relationships among social attributes and fecal GCMs, which provide an integrated measure of stress hormone production over time (Millspaugh & Washburn 2004, Keay et al. 2006). We expected differential responses among age-sex groups.

To be consistent with a social stressor hypothesis, we expected high values of received agonism to be positively associated with fecal GCMs. High values of agonistic initiation could be positively associated with fecal GCMs if involvement in agonistic interactions is stressful, or they could be negatively associated if animals that are less stressed are the ones initiating more agonistic behavior. Larger social group size could be associated with higher fecal GCMs if having more group members constitutes a stressor (Dunbar 1988). These patterns may be most pronounced in adult males, which compete for females and in which dominance rank is a significant predictor of reproductive success (Huang et al. 2011).

To be consistent with a social buffering hypothesis (e.g., in primates—Cohen et al. 1992, Das et al. 1998), we expect high values of received affiliation to be negatively associated with fecal GCMs. High values of affiliative initiation could be positively associated with fecal GCMs if initiating affiliation also helps reduce stress, or they could be negatively associated if animals that are more stressed are the ones seeking more affiliation. Larger group size could be associated with lower fecal GCMs if group members help alleviate stress (Cohen et al. 1992, Das et al. 1998). These patterns may be most pronounced in female yellow-bellied marmots because female kin recruitment enhances reproductive success (Armitage & Schwarz 2000) and social cohesion influences female yearling dispersal decisions (Blumstein et al. 2009).

METHODS

Study system

Yellow-bellied marmots are large, facultatively social, hibernating ground squirrels found in high-altitude areas throughout western North America (Armitage 2003). Young remain in the natal colony for at least a year, after which almost all males and about half the females disperse (Armitage & Downhower 1974). Adult males are more likely to move among colonies and generally have higher mortality rates than adult females (Schwartz et al. 1998). The mating system is harem polygynous, with maternal recruitment of female offspring resulting in stable matriline within colonies (Armitage 1991a). There are distinct behavioral, physiological, and selective differences among age-sex groups (Armitage 1991a), and we expect consistent differences in the relationships among social attributes and fitness correlates in different age-sex groups.

From 2003-2008, we observed yellow-bellied marmots at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, where marmots are part of long-term research that began in 1962 (Schwartz et al. 1998, Ozgul et al. 2010). We regularly collected behavioral and physiological data for social attributes and fitness measures. Marmots were individually marked for identification, allowing us to record the initiator, recipient, social interaction type, location, and time of each

behavioral interaction (method details in Blumstein et al. 2009 and Wey & Blumstein 2010). Observations and trapping took place during mornings and afternoons when marmots were most active (Armitage 1991a), throughout the majority of the active season, approximately mid-April to mid-September.

Social attributes

Observed interactions were divided into affiliative and agonistic datasets, and we constructed social networks based on observations of four marmot colonies (Bench-River, Marmot Meadow, Picnic, Town) per year. Colonies are geographically distinct, and a sizeable portion of colony membership changes each year—mostly through births, deaths, and dispersal (Schwartz et al. 1998).

Therefore, we defined a network as a colony in a given year because interactions with members of other colonies are extremely rare (as in Wey & Blumstein 2010, Lea et al. 2010). Only individuals seen on more than 5 occasions in a year were included in networks, so as not to include transient animals. All interactions with clearly initiator and recipient were retained because even infrequent interactions may have meaningful outcomes (Wey & Blumstein 2010). Network measures (social attributes) were calculated in UCINET (see Borgatti et al. 2006 for citation and descriptions of specific calculations). The terminology for some of these measures varies in the literature. We use descriptive terms, and we note other commonly used terms in the descriptions below and in the Appendix.

Initiation and Reception

“Initiation” is the number of social partners to which a marmot directs behavior, while “Reception” is the number of social partners from which a marmot receives behavior. These attributes are equivalent to Out-degree and In-degree, respectively (Wasserman & Faust 1994, Wey et al. 2008) and reflect an absolute amount of interaction initiated or received. They are only relevant on a local level and do not account for overall network dynamics. Initiation represents the ability to affect other network members through direct interactions, whereas Reception represents the ability to be affected by other network members through direct interactions. If a fitness measure is associated with Initiation or Reception, that measure is dependent upon the number of social partners or the absolute number of interactions with which that individual was involved.

Expansiveness and Attractiveness

“Expansiveness” is the relative amount of interaction initiated, and “Attractiveness” is the relative amount of interaction received (terms from sociology—Skvoretz & Faust 1999; also see Wey & Blumstein 2010 for previous use in this system). These measures are calculated after controlling for overall network characteristics of size, density, and reciprocity. Similar to Initiation and Reception, Expansiveness and Attractiveness are based only on direct interactions

and thus represent limited, local processes. However, Expansiveness and Attractiveness say more about how an individual acts compared to the others in the group, and do not represent an absolute amount of interaction. A focal individual can have a high value for Initiation (initiating many interactions in an absolute sense), but if others in the network also initiate many interactions, then that focal individual would have a low value for Expansiveness. If a fitness measure is associated with Expansiveness or Attractiveness, then the relative differences among the attributes of network members matters.

Out-closeness and In-closeness

In all but very small animal social networks, there will likely be network members that are not directly connected to each other. However, individuals may also be connected to, and therefore influence or be influenced by, others in the network through indirect connections. Social attributes that incorporate indirect interactions reflect an individual's connectedness in the overall network rather than only on a local level (as with Initiation, Reception, Expansiveness, and Attractiveness).

“Out-closeness” is an individual's potential to reach and influence others in the network through both direct and indirect connections originating from it, while “In-closeness” is an individual's potential to be reached and influenced by others in the network through both direct and indirect connections terminating at it (Wasserman & Faust 1994; see also Wey & Blumstein 2010 for previous use of

these measures in this system). If a fitness correlate is associated with Out-closeness or In-closeness, it implies that indirect connections matter. The particular patterns and effects of Out-closeness and In-closeness may be expected to be less general than those of direct interactions.

Group size

We also measured group size based on association indexes determined by spatial overlap in burrow use, calculated in the program SOCPROG (Whitehead 2009). Clusters of individuals with > 0.5 “simple ratio” association index were considered part of the same group (Nanayakkara & Blumstein 2003). This spatially based measure of group size was included in statistical models and compared to interaction-based social attributes. Group size may influence fitness independently from or in addition to effects of specific social attributes. Group size should have some absolute effect that is the same across different groups.

Fitness measures

Annual Reproductive Success

For adult marmots, we determined the number of offspring assigned to each individual each year using a comprehensive pedigree, described in Blumstein et al. (2010) and Olson & Blumstein (2010). Multilocus genotypes and the program CERVUS (Kalinowski et al. 2007) were used to assign parentage to 1006 offspring

at 95% confidence, and 5 at 80% confidence. In 17 cases, marmots were assigned parentage from behavioral observations alone.

Parasites

We examined both ectoparasites and endoparasites because we expected them to have different infection dynamics. To study ectoparasites, in 2007 and again in 2008, we attempted to comb marmots once every two weeks during trapping and counted fleas (*Thrassis stanfordi*, Van Vuren 1996) that were displaced onto a white flannel cloth. We converted this absolute number of fleas into fleas/kg to account for differential exposure to fleas as a function of body size, and we averaged these values for each individual to obtain a yearly index of flea infection. To examine endoparasites, from 2003-2008, we collected feces from marmots that defecated in traps, and performed fecal floats using Ova Float™ Zn 118 (zinc sulfate heptahydrate) on up to one sample per individual per month. Wet slides were then scored for presence of three fecal-orally transmitted intestinal parasites: *Eimeria* spp., *Entamoeba* sp., and *Ascaris* sp. Our measure of parasite diversity therefore reflected the number of parasite species detected for each individual in a given year.

Stress

From 2003-2008, we extracted and measured fecal glucocorticoid metabolites (GCM) from frozen samples (up to one sample per individual per month), as described in Blumstein et al. (2006). We use these GCM levels as our assay of baseline levels of stress, rather than response to an acute stressor, which are distinct (Romero 2004), and we only included fecal samples collected in the morning in analysis to control for daily glucocorticoid fluctuations (Blumstein et al. 2006). Though reproductive status can affect glucocorticoid levels (Reeder & Kramer 2005), this pattern has not been observed in yellow-bellied marmots (Armitage 1991b, Blumstein et al. 2006), so we do not specifically control for reproductive status. We averaged GCM for each individual to obtain a yearly index of basal stress.

Analysis

For all fitness measures except flea counts, we performed separate analyses for each age-sex class: adult females, adult males, yearling females, and yearling males. For analyses involving adults, individuals were present in multiple years. To account for this dependency, we fitted linear mixed effects models in R (R Development Core Team 2009) with the lme4 package (Bates & Maechler 2009) and included random intercepts for individuals. For analyses involving yearlings, we fitted general linear models in SPSS GradPack 16.0.2 (SPSS Inc. 2007). In all

analyses, we included fixed effects of year and colony to control for environmental variation, social group, and a social attribute. By putting social attributes and group size in the same model, we should be able to distinguish the contribution of each on a given fitness correlate. For flea counts (which came from only two years of data and had a smaller sample size), we included all age-sex classes in the same analyses and added fixed effects of age and sex. There were no significant age*sex interactions, so we omitted interactions from final analyses. Several variables were log10 transformed: annual number of offspring for males, number of fleas, and fecal GCM for all age-sex groups. We thus fit models with all combinations of fitness outcome by social attributes to examine broad patterns of variation.

As alternate methods to assess the utility of this attribute-based approach, we used comparisons of Akaike information criterion (AIC; Akaike 1974) values calculated in R and estimated R^2 values for partial models with social attributes and social group size. We ran a null model with no social factors (i.e., including only year, colony, and intercept; and age and sex for models of flea infection) and partial models with each social variable of interest (individual social attributes and group size) added to the null model. We then regressed predicted against observed values for each model and looked at the changes in R^2 values between the partial and null models.

RESULTS

We used a total of 9 652 affiliative interactions and 2 013 agonistic interactions in respective networks, from 4 845 hours of observation. Our final dataset included 357 individuals and 676 total cases: 272 on adult females, 105 on adult males, 138 on yearling females, and 161 on yearling males. Specific analyses were performed on subsets of these individuals for which relevant information was available. We present full model results in Tables 4-1 through 4-11, except for year and colony effects, which we do not interpret. We interpret significant effects if $P < 0.05$ below. AIC values and changes in R^2 are presented in Appendix B.

Annual Reproductive Success

For females, social group size, direct affiliative interactions, and both direct and indirect agonistic interactions were associated with larger litters (Table 4-1, Appendices C and D). Females in larger social groups had bigger litters (Estimates ranged from 0.021 - 0.035, all $P < 0.01$). Females with higher affiliative In-closeness had more offspring (Estimate = 0.008, $P = 0.045$). Females with higher agonistic Initiation and Out-closeness also had more offspring (Initiation: Estimate = 0.051, $P = 0.033$; Out-closeness: Estimate = 0.009, $P = 0.017$). Females that had higher affiliative Expansiveness had fewer offspring (Estimate = -0.206, $P < 0.001$). Other measured social attributes were not associated with litter size in

females. R^2 values for social attributes variables that were significantly associated with annual reproductive success in adult females were systematically larger than R^2 values for social group size. However, in some, but not all cases, an information theoretic approach suggests that they were not substantially better ($\Delta AIC < 2.0$; Figure 4-1a, Appendix B).

Social group size was not associated with male annual reproductive success (all $P > 0.05$), but males that initiated and received relatively more direct affiliative interactions and that initiated more direct agonistic interactions had higher annual fitness (Table 4-2, Appendices E and F). Males with higher affiliative Expansiveness scores had more offspring (Estimate = 0.084, $P = 0.042$). Males with higher affiliative Reception had fewer offspring (Estimate = -0.119, $P = 0.035$), while those with higher agonistic Initiation scores had more offspring (Estimate = 0.027, $P = 0.009$). Other social attributes were not associated with annual reproductive success in males. Social attributes variables that were significantly associated annual reproductive success for annual reproductive success in adult males did not always add more explanatory value to partial statistical models than social group size did, but models with social attributes fit better than a model with social group size (Figure 4-1b, Appendix B).

Parasites

A number of social attributes, both affiliative and agonistic, were negatively associated with number of fleas (Table 4-3, Appendices G and H). Marmots with higher affiliative Initiation, Reception, and In-closeness had fewer fleas (Initiation: Estimate = -0.016, $P = 0.042$; Reception: Estimate = - 0.023, $P = 0.009$; In-closeness: Estimate = -0.005, $P = 0.007$). Those with higher agonistic Initiation and Out-closeness had fewer fleas (Initiation: Estimate = -0.018, $P = 0.040$; Out-closeness: Estimate = -0.004, $P = 0.047$). Interestingly, social group size was not associated with the number of ectoparasites (all $P > 0.05$). Males generally had more fleas than females (in 8 of 12 analyses; Estimates ranged from 0.084 – 0.111, $0.013 < P < 0.051$). Other social attributes were not associated with number of fleas. Social attributes that were significantly associated with fleas/kg in all age-sex groups added more explanatory value to partial statistical models than social group size, and models with social attributes typically fit better than a model with social group size (Figure 4-2).

Neither measured social attributes, nor group size, explained the diversity of gut parasites (all $P > 0.05$; Tables 4-4 through 4-7, Appendices I through P). Two intestinal parasites (*Eimeria* spp. and *Entamoeba* sp.) were extremely common, and thus, there was limited variation to explain. (73.6% of individuals had 2 parasites, 17.3% had all 3, 8.9% had 1, and 0.2% had 0.)

Stress

There were a number of significant relationships among social attributes and fecal GCM levels in adult males (Table 4-8, Appendices Q and R). The general trend was that more social males (as measured by multiple affiliative and agonistic attributes) had lower basal GC levels. Specifically, males with higher affiliative Out-closeness and In-closeness had lower fecal GCM levels (Out-closeness: Estimate = -0.007, $P = 0.001$; In-closeness: Estimate = -0.006, $P = 0.007$). Similarly, males with higher agonistic Initiation, Expansiveness, and Out-closeness had lower fecal GCM levels (Initiation: Estimate = -0.017, $P = 0.034$; Expansiveness: Estimate = -0.082, $P = 0.014$; Out-closeness: Estimate = -0.005, $P = 0.003$). Most social attributes that were significantly associated with fecal GCMs in adult males added more explanatory value to partial statistical models than social group size did, and models with social attributes were typically fit better than a model with social group size (Figure 4-3, Appendix B).

Social attributes were not significantly associated with fecal GCMs in any other age-sex group (all $P > 0.05$; Tables 4-9 through 4-11, Appendices S through X). In one analysis (with agonistic Expansiveness) in yearling females, social group size was positively associated with fecal GCMs (Estimate = 0.024, $P = 0.041$); however, this analysis had an extremely small sample size ($N = 17$), so we do not interpret this result.

DISCUSSION

Taken together we have demonstrated that novel insights about the adaptive value of sociality can be obtained by adopting an attribute-based social network analysis. Indeed, in many cases, these network-derived attributes explained more variation than did group size—a measure typically used to study the adaptive basis of sociality (e.g., in primates—Dunbar 2003; in cliff swallows, *Hirundo pyrrhonota*—Brown & Brown 1996; and in black-tailed prairie dogs, *Cynomys ludovicianus*—Hoogland 1995). Below, we discuss insights about marmot sociality obtained and suggest broader applicability of this attribute-based approach.

Annual Reproductive Success

Both affiliative and agonistic attributes seemingly played an important role in female and male offspring production. Females that received more direct and indirect affiliation, but that initiated more direct and indirect agonism, had larger litter sizes. In other words, successful females were the foci of incoming affiliation and also radiated agonism into the network. Males that initiated high relative amounts of affiliation (were more gregarious) and high absolute amounts of agonism (initiated more local agonistic interactions) had higher annual reproductive success, suggesting a greater importance of cohesion in males than previously thought. Thus both females and males employed reproductive strategies

that incorporated different attributes of affiliation and agonism, an idea consistent with other studies (Armitage 1991a, Armitage 1998, Lea et al. 2010). However, unlike Armitage (1991a), we focused on interaction-based social attributes, and unlike Lea et al. (2010), we focused on a different combination of social attributes and analyzed them annually for females and males separately.

Contrary to expectations and findings in a study of the correlates of lifetime reproductive success (Lea et al. 2010), there was apparently no annual reproductive cost associated with receiving more agonism. Also surprisingly, females that initiated higher relative amounts of affiliation had fewer offspring each year, and males that received relatively more affiliation had lower reproductive success. It is possible that females with larger litters devoted less time and energy to initiating affiliation, so the most gregarious females in the network were the ones who cared for the fewest offspring. For males, association with adult females, which is critical to male reproductive success, generally only occurs at age three or older (Armitage 1991a), so it may be that the youngest adult males, with the lowest reproductive success, are more actively initiating affiliation. However, testing this hypothesis would require better data on exact adult male ages, which is problematic given that most adult males are first detected as adult immigrants.

Social group size was not an important determinant of male annual reproductive success, but females in larger groups had larger litters. More successful females are likely ones that have more female relatives in the same

colony (Armitage 1991a, 1998), and their young from the previous year may also remain in relatively close proximity. Examining social attributes in conjunction with group size contributes novel understanding to what we previously knew from studies of group size and dominance in this system. For example, dominance is an important predictor of annual reproductive success in males but not in females (Huang et al. 2011), but agonistic social attributes, which reflect patterns of agonistic interactions regardless of winner-loser outcomes, were important for both males and females.

Parasites

Higher values of social attributes were not associated with increased parasitism by ecto- or endoparasites; thus we found no evidence for the hypothesis that parasites are a cost of increased sociality at the individual level, compared with the pattern seen at the group or species level in many systems (Côté & Poulin 1995, Altizer et al. 2003). Ectoparasite infection revealed some support for the idea of social compensation for parasites, which has been previously suggested (Moore 2002, Altizer et al. 2003, Bordes et al. 2007). Marmots that received more absolute direct and indirect interactions had fewer fleas. Though allogrooming represented a small portion (~ 4%) of observed affiliation, even a small amount of allogrooming could make a significant difference, and there could be a high frequency of unobserved allogrooming underground. Surprisingly, marmots that initiated more direct

affiliative and direct and indirect agonistic interactions also had fewer fleas. The mechanism for this is not readily apparent, though we speculate that it may be related to condition, which is positively correlated to interaction rates (Wey & Blumstein, unpublished data).

Social group size was not significantly associated with fleas or intestinal parasites. Group size is a commonly used correlate for sociality, and while there is often a trend of increasing parasitism in larger groups, the relationship between these two variables is not always so straightforward (e.g., in primates—Nunn & Altizer 2006; in other animals—Krause & Ruxton 2002). Previous studies on ectoparasites in alpine marmots (*Marmota marmota*; Arnold & Lichtenstein 1993) and yellow-bellied marmots (Van Vuren 1996) also concluded that they were not a cost of sociality per se, though colonial hibernation affected ectoparasite loads in the latter study. While previous studies of sociality and parasites in marmots have not specifically focused on internal parasites, the routine infections of *Eimeria* spp. and *Entamoeba* sp., and the lack of any social attribute effects on intestinal parasites may suggest that they are unavoidably prevalent in this population, or that they are not extremely costly to the host. It is possible that measures of parasite load (rather than diversity) might detect relationships with social attributes.

Stress

In general, we found no support for the social stressor hypothesis. Agonistic social attributes were not positively associated with fecal GCM, and in adult males, fecal GCM levels were negatively associated with several social attributes: agonistic Initiation, Out-closeness, and Expansiveness, as well as affiliative Out-closeness and In-closeness. The consistent negative relationships indicate that the males with the lowest basal stress levels were the most influential in agonistic networks and the best-connected in affiliative networks. As with the pattern seen with fleas, the association between low fecal GCMs and high initiation rates may be related to body condition, which is positively correlated to interaction rates (Wey & Blumstein, unpublished data). Interestingly, affiliative Out-closeness and In-closeness were associated with fecal GCMs, independent of affiliative Initiation and Reception, i.e., indirect interactions seemed to have an association independent of direct interactions. It is thus the further reaching connections throughout the network rather than local interactions that are important in this case.

These results also do not provide strong support for the social buffering hypothesis because high amounts of direct received affiliation were not generally associated with lower fecal GCM levels in any age-sex group. Social group size was not associated with fecal GCMs. Our results are somewhat inconsistent with Armitage (1991a), which reports an effect of social stressors on plasma glucocorticoids. However, fecal GCMs reflect composite stress hormone levels

integrated over a different time frame than plasma levels. Overall, social attributes had little explanatory power for fecal GCMs, except in adult males, implying that our measured social attributes were not explained in adult females or yearlings.

Conclusions

Adopting an attribute-based approach gave us novel insights into marmot sociality and suggests both value and caution in applying it to other taxa. Sociality is currently adaptive in facultatively social yellow-bellied marmots. We infer this because high values of social attributes were generally associated with benefits rather than costs. Future studies will permit us to understand if this is generally the case in other social systems, and if there are social systems in which sociality is not currently adaptive. These findings have implications for current selection pressures acting on social systems and possible directions of future evolution, especially considering that some social network traits are heritable (Lea et al. 2010). Furthermore, the adaptive value of sociality varies by age and sex. This will likely be the case in other social systems as well, and it highlights the importance of clearly considering sex differences and ontogenetic stage. These distinctions are important in numerous species and biological contexts.

In this study, indirect interactions and relative measures of interaction had few observable fitness effects, but whether this pattern holds for other systems remains to be tested. It may be that indirect connections would play a larger role in

more socially complex and cognitively developed species, which may be aware of and more intentionally use indirect connections. In human business networks, for instance, utilization of indirect connections is especially important for upward mobility (Granovetter 1973, Podolny & Baron 1997). In comparison with social group size, models with network attributes often had more explanatory value in terms of information criteria and estimated effect sizes and allowed us to distinguish sources of fitness outcomes. Overall, a social attribute-based approach has potential for more precisely understanding the adaptive value of sociality, but it remains to be seen if general inferences across systems can be made.

Table 4-1. Relationships among social attributes and annual reproductive success in adult females. The outcome variable for females was number of offspring in a given year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	<i>P</i> -value		Parameter	Estimate	<i>P</i> -value
N = 268	Intercept	0.603	0.012	N = 268	Intercept	0.519	0.031
IDs = 98	Social group size	0.028	0.001	IDs = 98	Social group size	0.022	0.006
	Initiation	-0.039	0.131		Initiation	0.051	0.033
N = 268	Intercept	0.561	0.020	N = 268	Intercept	0.653	0.008
IDs = 98	Social group size	0.023	0.004	IDs = 98	Social group size	0.025	0.002
	Reception	0.019	0.426		Reception	-0.050	0.237
N = 268	Intercept	0.540	0.026	N = 268	Intercept	0.500	0.037
IDs = 98	Social group size	0.022	0.008	IDs = 98	Social group size	0.023	0.004
	Out-closeness	0.005	0.159		Out-closeness	0.009	0.017
N = 268	Intercept	0.483	0.048	N = 268	Intercept	0.613	0.013
IDs = 98	Social group size	0.021	0.010	IDs = 98	Social group size	0.025	0.002
	In-closeness	0.008	0.045		In-closeness	-0.003	0.635
N = 194	Intercept	0.293	0.312	N = 153	Intercept	0.704	0.012
IDs = 78	Social group size	0.032	< 0.001	IDs = 70	Social group size	0.025	0.008
	Expansiveness	-0.206	< 0.001		Expansiveness	-0.045	0.376
N = 203	Intercept	0.604	0.024	N = 162	Intercept	0.425	0.153
IDs = 81	Social group size	0.031	< 0.001	IDs = 71	Social group size	0.035	< 0.001
	Attractiveness	0.028	0.506		Attractiveness	0.086	0.365

Table 4-2. Relationships among social attributes and annual reproductive success in adult males. The outcome variable was the log10 transformed number of offspring in a given year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	<i>P</i> -value		Parameter	Estimate	<i>P</i> -value
N = 55	Intercept	1.169	< 0.001	N = 55	Intercept	1.143	< 0.001
IDs = 26	Social group size	-0.008	0.459	IDs = 26	Social group size	-0.009	0.388
	Initiation	0.026	0.051		Initiation	0.027	0.009
N = 55	Intercept	1.208	< 0.001	N = 55	Intercept	1.218	< 0.001
IDs = 26	Social group size	0.000	0.897	IDs = 26	Social group size	0.001	0.821
	Reception	-0.006	0.968		Reception	-0.026	0.700
N = 55	Intercept	1.172	< 0.001	N = 55	Intercept	1.134	< 0.001
IDs = 26	Social group size	-0.004	0.697	IDs = 26	Social group size	-0.004	0.801
	Out-closeness	0.003	0.214		Out-closeness	0.004	0.124
N = 55	Intercept	1.214	< 0.001	N = 55	Intercept	1.248	< 0.001
IDs = 26	Social group size	0.001	0.906	IDs = 26	Social group size	0.001	0.751
	In-closeness	-0.003	0.992		In-closeness	-0.007	0.367
N = 47	Intercept	1.314	< 0.001	N = 41	Intercept	1.202	< 0.001
IDs = 23	Social group size	-0.007	0.570	IDs = 20	Social group size	-0.004	0.990
	Expansiveness	0.084	0.042		Expansiveness	0.073	0.109
N = 43	Intercept	1.000	< 0.001	N = 38	Intercept	1.083	0.002
IDs = 22	Social group size	-0.003	0.838	IDs = 22	Social group size	-0.003	0.804
	Attractiveness	-0.119	0.035		Attractiveness	-0.035	0.427

Table 4-3. Relationships among social attributes and number of fleas for all age-sex groups combined. The outcome variable was a log10 transformed average number of fleas/kg for that individual in a year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	<i>P</i> -value		Parameter	Estimate	<i>P</i> -value
N = 185	Intercept	-0.095	0.189	N = 185	Intercept	-0.097	0.184
IDs = 136	Age = Y	-0.031	0.514	IDs = 136	Age = Y	-0.092	0.082
	Sex = M	0.107	0.014		Sex = M	0.111	0.013
	Social group size	0.001	0.887		Social group size	0.000	0.982
	Initiation	-0.016	0.042		Initiation	-0.018	0.040
N = 185	Intercept	-0.068	0.347	N = 185	Intercept	-0.092	0.215
IDs = 136	Age = Y	-0.007	0.875	IDs = 136	Age = Y	-0.034	0.470
	Sex = M	0.085	0.048		Sex = M	0.094	0.031
	Social group size	0.001	0.891		Social group size	-0.002	0.713
	Reception	-0.023	0.009		Reception	-0.016	0.300
N = 185	Intercept	-0.096	0.191	N = 185	Intercept	-0.081	0.282
IDs = 136	Age = Y	-0.030	0.537	IDs = 136	Age = Y	-0.090	0.088
	Sex = M	0.089	0.039		Sex = M	0.102	0.021
	Social group size	0.001	0.859		Social group size	-0.001	0.915
	Out-closeness	-0.003	0.078		Out-closeness	-0.004	0.047
N = 185	Intercept	-0.050	0.515	N = 185	Intercept	-0.082	0.283
IDs = 136	Age = Y	-0.022	0.627	IDs = 136	Age = Y	-0.033	0.494
	Sex = M	0.084	0.051		Sex = M	0.091	0.040
	Social group size	0.000	0.930		Social group size	-0.002	0.661
	In-closeness	-0.005	0.007		In-closeness	-0.003	0.219
N = 161	Intercept	-0.112	0.100	N = 106	Intercept	-0.162	0.049
IDs = 124	Age = Y	-0.046	0.377	IDs = 88	Age = Y	-0.107	0.089
	Sex = M	0.048	0.240		Sex = M	0.068	0.196
	Social group size	-0.002	0.769		Social group size	0.002	0.625
	Expansiveness	-0.014	0.323		Expansiveness	-0.021	0.295
N = 158	Intercept	-0.101	0.188	N = 127	Intercept	-0.130	0.034
IDs = 121	Age = Y	-0.039	0.451	IDs = 108	Age = Y	-0.063	0.201
	Sex = M	0.058	0.210		Sex = M	0.063	0.198
	Social group size	-0.003	0.588		Social group size	-0.003	0.684
	Attractiveness	0.002	0.966		Attractiveness	-0.006	0.849

Table 4-4. Relationships among social attributes and intestinal parasite diversity in adult females. The outcome variable was a count of the types of parasites detected (0-3) in an individual in a given year. Results for year and colony are not shown, although these variables were included in the models.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	P-value		Parameter	Estimate	P-value
N = 195	Intercept	0.568	0.115	N = 195	Intercept	0.557	0.128
IDs = 82	Social group size	0.001	0.896	IDs = 82	Social group size	< 0.001	0.960
	Initiation	< 0.001	0.992		Initiation	0.005	0.839
N = 195	Intercept	0.569	0.115	N = 195	Intercept	0.555	0.125
IDs = 82	Social group size	< 0.001	0.960	IDs = 82	Social group size	< 0.001	0.968
	Reception	0.004	0.871		Reception	0.019	0.635
N = 195	Intercept	0.567	0.117	N = 195	Intercept	0.558	0.133
IDs = 82	Social group size	0.001	0.912	IDs = 82	Social group size	0.001	0.923
	Out-closeness	< 0.001	0.975		Out-closeness	0.001	0.907
N = 195	Intercept	0.550	0.133	N = 195	Intercept	0.568	0.119
IDs = 82	Social group size	< 0.001	0.990	IDs = 82	Social group size	0.001	0.890
	In-closeness	0.001	0.773		In-closeness	< 0.001	0.996
N = 154	Intercept	0.665	0.148	N = 129	Intercept	0.531	0.220
IDs = 69	Social group size	< 0.001	0.963	IDs = 64	Social group size	0.002	0.868
	Expansiveness	-0.016	0.743		Expansiveness	-0.026	0.691
N = 162	Intercept	0.549	0.194	N = 131	Intercept	0.536	0.206
IDs = 73	Social group size	< 0.001	0.992	IDs = 63	Social group size	0.001	0.905
	Attractiveness	0.005	0.915		Attractiveness	0.038	0.622

Table 4-5. Relationships among social attributes and intestinal parasite diversity in adult males. The outcome variable was a count of the types of parasites detected (0-3) in an individual in a given year. Results for year and colony are not shown, although these variables were included in the models.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	<i>P</i> -value		Parameter	Estimate	<i>P</i> -value
N = 62	Intercept	-0.077	0.919	N = 62	Intercept	-0.056	0.941
IDs = 39	Social group size	-0.007	0.660	IDs = 39	Social group size	-0.006	0.710
	Initiation	0.017	0.542		Initiation	0.011	0.626
N = 62	Intercept	0.007	0.992	N = 62	Intercept	0.015	0.984
IDs = 39	Social group size	-0.004	0.800	IDs = 39	Social group size	-0.004	0.789
	Reception	0.012	0.824		Reception	0.028	0.657
N = 62	Intercept	-0.034	0.965	N = 62	Intercept	0.007	0.993
IDs = 39	Social group size	-0.006	0.746	IDs = 39	Social group size	-0.004	0.817
	Out-closeness	0.002	0.730		Out-closeness	0.001	0.861
N = 62	Intercept	0.027	0.972	N = 62	Intercept	0.003	0.997
IDs = 39	Social group size	-0.003	0.829	IDs = 39	Social group size	-0.003	0.826
	In-closeness	0.001	0.904		In-closeness	0.003	0.770
N = 49	Intercept	-0.012	0.988	N = 43	Intercept	-0.043	0.954
IDs = 30	Social group size	-0.001	0.974	IDs = 26	Social group size	0.002	0.911
	Expansiveness	0.014	0.883		Expansiveness	0.010	0.899
N = 46	Intercept	-0.024	0.974	N = 39	Intercept	0.256	0.742
IDs = 28	Social group size	0.001	0.963	IDs = 26	Social group size	-0.003	0.852
	Attractiveness	-0.034	0.765		Attractiveness	0.122	0.447

Table 4-6. Relationships among social attributes and intestinal parasite diversity in yearling females. The outcome variable was a count of the types of parasites detected (0-3) in an individual in a given year. Results for year and colony are not shown, although these variables were included in the models.

Affiliative attributes				Agonistic attributes			
	Parameter	B	P-value		Parameter	B	P-value
N = 78	Intercept	2.063	< 0.001	N = 78	Intercept	2.066	< 0.001
	Social group size	-0.006	0.619		Social group size	0.000	0.965
	Initiation	0.029	0.326		Initiation	0.082	0.157
N = 78	Intercept	2.086	< 0.001	N = 78	Intercept	2.081	< 0.001
	Social group size	-0.005	0.671		Social group size	-0.003	0.796
	Reception	0.022	0.472		Reception	0.054	0.183
N = 78	Intercept	2.008	< 0.001	N = 78	Intercept	2.104	< 0.001
	Social group size	-0.006	0.636		Social group size	-0.001	0.940
	Out-closeness	0.007	0.282		Out-closeness	0.005	0.514
N = 78	Intercept	2.018	< 0.001	N = 78	Intercept	2.052	< 0.001
	Social group size	-0.004	0.710		Social group size	-0.001	0.893
	In-closeness	0.006	0.394		In-closeness	0.008	0.262
N = 74	Intercept	2.127	< 0.001	N = 37	Intercept	2.166	< 0.001
	Social group size	-0.004	0.693		Social group size	0.024	0.303
	Expansiveness	-0.011	0.840		Expansiveness	-0.024	0.831
N = 73	Intercept	2.055	< 0.001	N = 67	Intercept	1.911	< 0.001
	Social group size	-0.005	0.620		Social group size	-0.006	0.597
	Attractiveness	-0.065	0.225		Attractiveness	0.103	0.537

Table 4-7. Relationships among social attributes and intestinal parasite diversity in yearling males. The outcome variable was a count of the types of parasites detected (0-3) in an individual in a given year. Results for year and colony are not shown, although these variables were included in the models.

Affiliative attributes				Agonistic attributes			
	Parameter	B	P-value		Parameter	B	P-value
N = 93	Intercept	1.945	< 0.001	N = 93	Intercept	1.864	< 0.001
	Social group size	0.001	0.908		Social group size	0.002	0.796
	Initiation	0.007	0.690		Initiation	0.058	0.112
N = 93	Intercept	1.949	< 0.001	N = 93	Intercept	1.931	< 0.001
	Social group size	0.002	0.803		Social group size	0.003	0.747
	Reception	0.003	0.875		Reception	0.014	0.665
N = 93	Intercept	1.894	< 0.001	N = 93	Intercept	1.862	< 0.001
	Social group size	0.001	0.905		Social group size	0.002	0.819
	Out-closeness	0.004	0.372		Out-closeness	0.008	0.092
N = 93	Intercept	1.902	< 0.001	N = 93	Intercept	1.914	< 0.001
	Social group size	0.000	0.986		Social group size	0.002	0.815
	In-closeness	0.004	0.457		In-closeness	0.004	0.526
N = 90	Intercept	2.048	< 0.001	N = 56	Intercept	1.950	< 0.001
	Social group size	0.000	0.974		Social group size	0.012	0.255
	Attractiveness	0.017	0.717		Expansiveness	0.127	0.046
N = 89	Intercept	2.054	< 0.001	N = 79	Intercept	2.039	< 0.001
	Social group size	0.001	0.851		Social group size	0.001	0.887
	Attractiveness	0.026	0.583		Attractiveness	0.093	0.209

Table 4-8. Relationships among social attributes and morning fecal GCM levels in adult males. The outcome variable was the log10 transformed average fecal glucocorticoid metabolite (ng/g) levels per individual in a year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	<i>P</i> -value		Parameter	Estimate	<i>P</i> -value
N = 44	Intercept	2.296	< 0.001	N = 44	Intercept	2.263	< 0.001
IDs = 30	Social group size	0.005	0.440	IDs = 30	Social group size	0.005	0.409
	Initiation	-0.017	0.061		Initiation	-0.017	0.034
N = 44	Intercept	2.304	< 0.001	N = 44	Intercept	2.268	< 0.001
IDs = 30	Social group size	0.004	0.542	IDs = 30	Social group size	0.002	0.754
	Reception	-0.026	0.071		Reception	-0.025	0.127
N = 44	Intercept	2.363	< 0.001	N = 44	Intercept	2.288	< 0.001
IDs = 30	Social group size	0.008	0.117	IDs = 30	Social group size	0.005	0.293
	Out-closeness	-0.007	0.001		Out-closeness	-0.005	0.003
N = 44	Intercept	2.299	< 0.001	N = 44	Intercept	2.289	< 0.001
IDs = 30	Social group size	0.006	0.250	IDs = 30	Social group size	0.002	0.704
	In-closeness	-0.006	0.007		In-closeness	-0.004	0.079
N = 40	Intercept	2.253	< 0.001	N = 34	Intercept	2.261	< 0.001
IDs = 27	Social group size	0.005	0.495	IDs = 22	Social group size	0.005	0.377
	Expansiveness	-0.044	0.171		Expansiveness	-0.082	0.014
N = 37	Intercept	2.092	< 0.001	N = 28	Intercept	2.147	< 0.001
IDs = 25	Social group size	0.006	0.377	IDs = 19	Social group size	0.006	0.398
	Attractiveness	0.016	0.857		Attractiveness	0.016	0.831

Table 4-9. Relationships among social attributes and morning fecal GCM levels in adult females. The outcome variable was the log10 transformed average fecal glucocorticoid metabolite (ng/g) levels per individual in a year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

Affiliative attributes				Agonistic attributes			
	Parameter	Estimate	<i>P</i> -value		Parameter	Estimate	<i>P</i> -value
N = 177	Intercept	2.298	< 0.001	N = 177	Intercept	2.294	< 0.001
IDs = 74	Social group size	-0.001	0.777	IDs = 74	Social group size	-0.001	0.752
	Initiation	0.006	0.295		Initiation	0.008	0.228
N = 177	Intercept	2.297	< 0.001	N = 177	Intercept	2.292	< 0.001
IDs = 74	Social group size	0.000	0.842	IDs = 74	Social group size	0.001	0.728
	Reception	0.005	0.388		Reception	-0.002	0.802
N = 177	Intercept	2.291	< 0.001	N = 177	Intercept	2.289	< 0.001
IDs = 74	Social group size	0.000	0.920	IDs = 74	Social group size	0.000	0.812
	Out-closeness	0.001	0.478		Out-closeness	0.001	0.231
N = 177	Intercept	2.287	< 0.001	N = 177	Intercept	2.292	< 0.001
IDs = 74	Social group size	-0.001	0.750	IDs = 74	Social group size	0.001	0.774
	In-closeness	0.001	0.312		In-closeness	0.000	0.891
N = 136	Intercept	2.281	< 0.001	N = 115	Intercept	2.319	< 0.001
IDs = 61	Social group size	0.001	0.758	IDs = 54	Social group size	0.002	0.426
	Expansiveness	-0.010	0.388		Expansiveness	0.007	0.651
N = 143	Intercept	2.303	< 0.001	N = 121	Intercept	2.299	< 0.001
IDs = 65	Social group size	0.002	0.404	IDs = 59	Social group size	0.001	0.839
	Attractiveness	0.025	0.050		Attractiveness	0.011	0.578

Table 4-10. Relationships among social attributes and morning fecal GCM levels in yearling females. The outcome variable was the log10 transformed average fecal glucocorticoid metabolite (ng/g) levels per individual in a year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

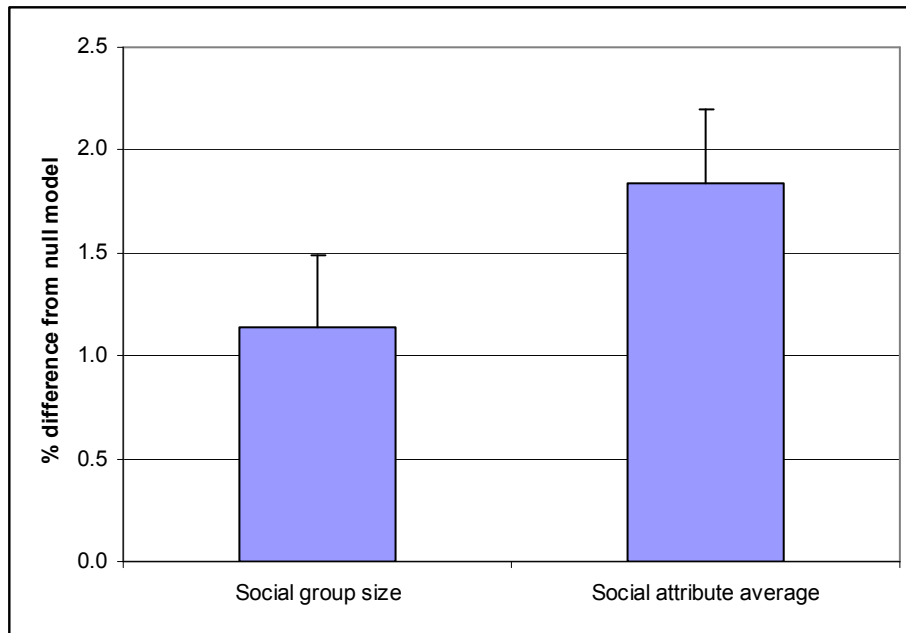
Affiliative attributes				Agonistic attributes			
	Parameter	B	<i>P</i> -value		Parameter	B	<i>P</i> -value
N = 78	Intercept	2.063	< 0.001	N = 78	Intercept	2.066	< 0.001
	Social group size	-0.006	0.619		Social group size	0.000	0.965
	Initiation	0.029	0.326		Initiation	0.082	0.157
N = 78	Intercept	2.086	< 0.001	N = 78	Intercept	2.081	< 0.001
	Social group size	-0.005	0.671		Social group size	-0.003	0.796
	Reception	0.022	0.472		Reception	0.054	0.183
N = 78	Intercept	2.008	< 0.001	N = 78	Intercept	2.104	< 0.001
	Social group size	-0.006	0.636		Social group size	-0.001	0.940
	Out-closeness	0.007	0.282		Out-closeness	0.005	0.514
N = 78	Intercept	2.018	< 0.001	N = 78	Intercept	2.052	< 0.001
	Social group size	-0.004	0.710		Social group size	-0.001	0.893
	In-closeness	0.006	0.394		In-closeness	0.008	0.262
N = 74	Intercept	2.127	< 0.001	N = 37	Intercept	2.166	< 0.001
	Social group size	-0.004	0.693		Social group size	0.024	0.303
	Expansiveness	-0.011	0.840		Expansiveness	-0.024	0.831
N = 73	Intercept	2.055	< 0.001	N = 67	Intercept	1.911	< 0.001
	Social group size	-0.005	0.620		Social group size	-0.006	0.597
	Attractiveness	-0.065	0.225		Attractiveness	0.103	0.537

Table 4-11. Relationships among social attributes and morning fecal GCM levels in yearling males. The outcome variable was the log10 transformed average fecal glucocorticoid metabolite (ng/g) levels per individual in a year. Results for year and colony are not shown, although these variables were included in the models. Associations with $P < 0.05$ are in bold.

Affiliative attributes				Agonistic attributes			
	Parameter	B	<i>P</i> -value		Parameter	B	<i>P</i> -value
N = 93	Intercept	1.945	< 0.001	N = 93	Intercept	1.864	< 0.001
	Social group size	0.001	0.908		Social group size	0.002	0.796
	Initiation	0.007	0.690		Initiation	0.058	0.112
N = 93	Intercept	1.949	< 0.001	N = 93	Intercept	1.931	< 0.001
	Social group size	0.002	0.803		Social group size	0.003	0.747
	Reception	0.003	0.875		Reception	0.014	0.665
N = 93	Intercept	1.894	< 0.001	N = 93	Intercept	1.862	< 0.001
	Social group size	-0.001	0.905		Social group size	0.002	0.819
	Out-closeness	0.004	0.372		Out-closeness	0.008	0.092
N = 93	Intercept	1.902	< 0.001	N = 93	Intercept	1.914	< 0.001
	Social group size	0.000	0.986		Social group size	0.002	0.815
	In-closeness	0.004	0.457		In-closeness	0.004	0.526
N = 90	Intercept	2.048	< 0.001	N = 56	Intercept	1.950	< 0.001
	Social group size	0.000	0.974		Social group size	0.012	0.255
	Attractiveness	0.017	0.717		Expansiveness	0.127	0.046
N = 89	Intercept	2.054	< 0.001	N = 79	Intercept	2.039	< 0.001
	Social group size	0.001	0.851		Social group size	0.001	0.887
	Attractiveness	-0.026	0.583		Attractiveness	-0.093	0.209

Figure 4-1. Percent difference in R^2 of observed vs. predicted value regressions between partial models predicting annual reproductive success, including either social group size or individual social attributes, and a null model without social factors, in a) adult females, and b) adult males. Only social attributes that were significantly associated with annual reproductive success are included, and the percent differences are averaged across social attributes. Error bars are standard errors.

(a)



(b)

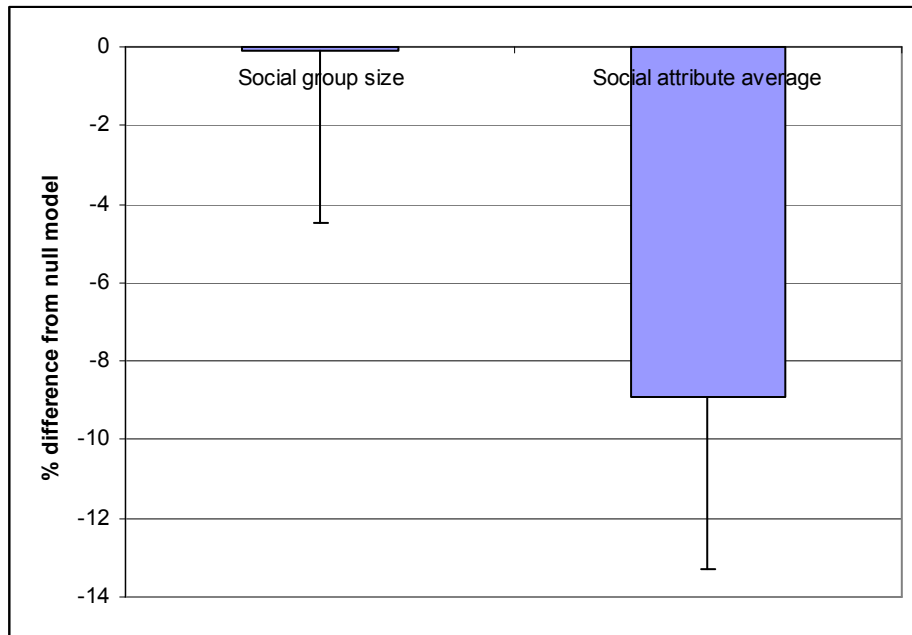


Figure 4-2. Percent difference in R^2 of observed vs. predicted value regressions between partial models predicting fleas/kg in all age-sex groups, including either social group size or individual social attributes, and a null model without social factors. Only social attributes that were significantly associated with annual reproductive success are included, and the percent differences are averaged across social attributes. Error bars are standard errors.

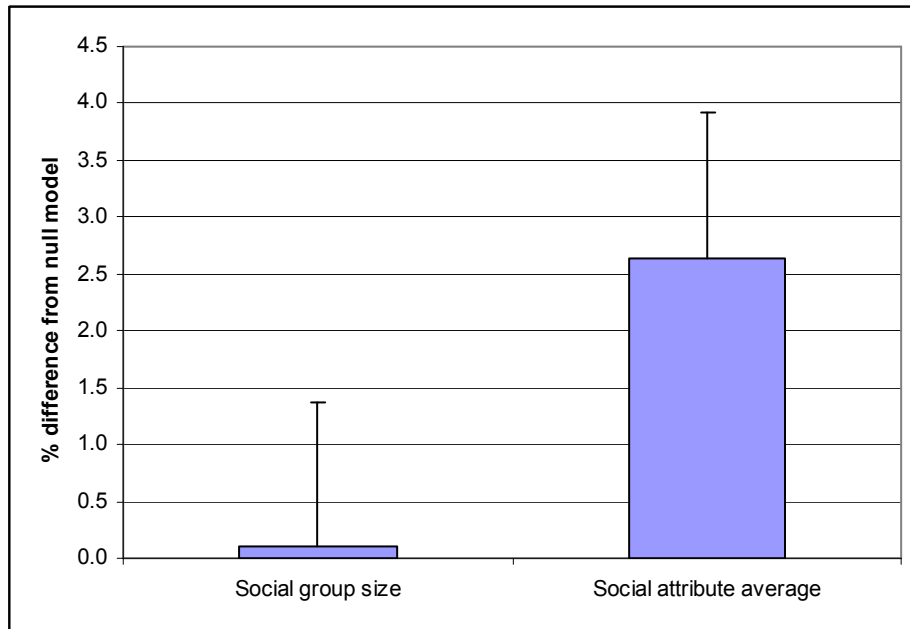
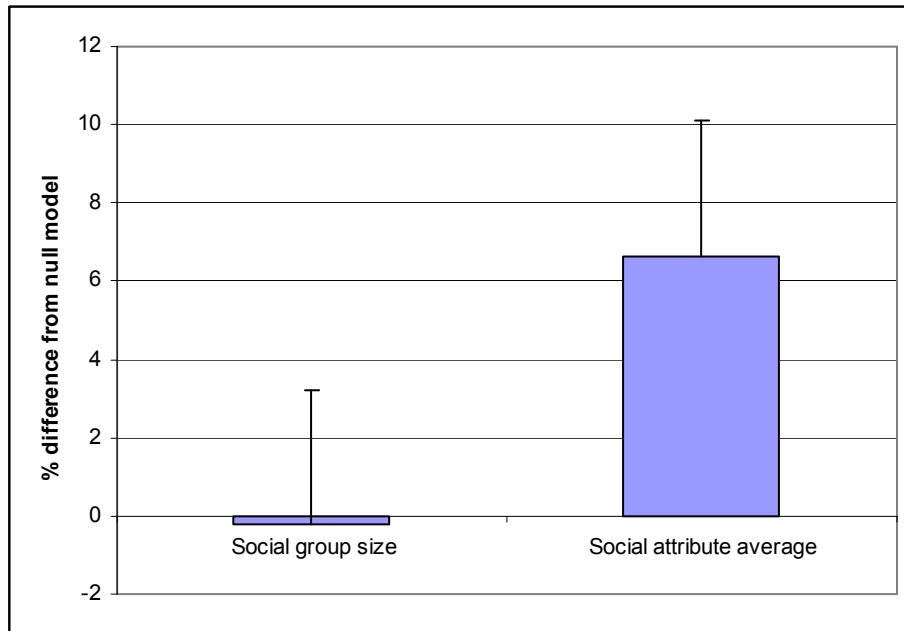


Figure 4-3. Percent difference in R^2 of observed vs. predicted value regressions between partial models predicting fecal GCM levels in adult males, including either social group size or individual social attributes, and a null model without social factors. Only social attributes that were significantly associated with annual reproductive success are included, and the percent differences are averaged across social attributes. Error bars are standard errors.



Appendix A. Network terminology and details on social attributes

The individual units of a network are called *nodes*, *vertices*, *points*, or *actors*, and the connections between units are called *ties*, *edges*, or *links*. In the current study, nodes represent individual marmots, and the ties represent social interactions, so we simply refer to marmots and their interactions throughout the paper. For analysis in programs such as UCINET, networks are input as matrices. Marmot networks were $N \times N$ adjacency matrices (N = number of marmots in the colony), with initiators as rows and recipients as columns.

Networks can be *symmetric* (marmot A connected to marmot B is equivalent to B connected to A) or *non-symmetric* (also called *directed*; A connected to B is not equivalent to B connected to A). We used non-symmetric networks because we were interested in the direction of initiation and reception; thus marmot A initiating an interaction to marmot B is distinct from marmot B initiating an interaction to A. Networks can also be *binary* or *valued*, based on whether the connections are unweighted or weighted. While we started with valued networks, in which the connections reflected numbers of interactions between pairs of marmots, we calculated final network measures (i.e., social attributes) based on the binary conversions. Out-closeness, In-closeness, Expansiveness, and Attractiveness are defined for binary networks. Binary and valued versions of Reception and Initiation were highly correlated resulted in very similar outcomes, so we used the

binary versions as the simpler option. For more information and discussion about network analysis, see Wasserman & Faust (1994), Borgatti et al. (2006), Croft et al. 2008, and Wey et al. (2008).

Initiation and Reception (Out-degree and In-degree)

In a binary symmetric network, the Degree of a node is the number of ties it has or the number of adjacent nodes (i.e., the row or column sum in an adjacency matrix).

In a non-symmetric network, Out-degree is the number of ties originating from a node (i.e., the row sum in an adjacency matrix), and In-degree is the number of ties terminating at a node (i.e., the column sum in an adjacency matrix). In this study, we refer to Out-degree and In-degree as Initiation and Reception, respectively.

Also see Freeman (1979) and Friedkin (1991) for further discussion of Degree.

Out-closeness and In-closeness

In a symmetric network, Closeness is traditionally defined as the reciprocal of the sum of the geodesic distances from a focal node to all other nodes in the network (Freeman 1979), where a geodesic is the shortest path between two nodes.

Therefore, the more closely connected a node is to every other node in the network (i.e., the shorter the path lengths connecting that node to other nodes), the larger the node's Closeness. However, in this definition, if a network is fragmented (i.e., there are unconnected nodes in the network), Closeness is undefined because the

distance between unconnected nodes is infinite. Because some of the marmot networks were fragmented, we used a modified version of Closeness, in which the reciprocals are taken before summing, and so the infinite distances contribute a zero value instead of being undefined. In a non-symmetric network, Out-closeness and In-closeness are calculated including only paths that originate from or terminate at the focal node, respectively, and do not include any reversals in direction. Also see Freeman (1979) and Friedkin (1991) for further discussion of Closeness.

Expansiveness and Attractiveness

In a binary, asymmetric network, Expansiveness and Attractiveness (also called Productivity and Popularity, respectively; Borgatti et al. 2006) are calculated by fitting Holland & Leinhardt's (1982) p_1 models, or exponential random graph models (ERGM; see Robins et al. 2007 for an introduction). Generally speaking, this models the probability of mutual, asymmetric, or absent interactions in the network while controlling for overall network density (the number of interactions present relative to the number that could exist for a network of that size) and overall network reciprocity (tendency of interactions to be mutual: if A interacted with B, then B interacted with A). For each individual in the network, α and β parameters of relative initiation and reception are calculated, and we refer to these as Expansiveness and Attractiveness, respectively.

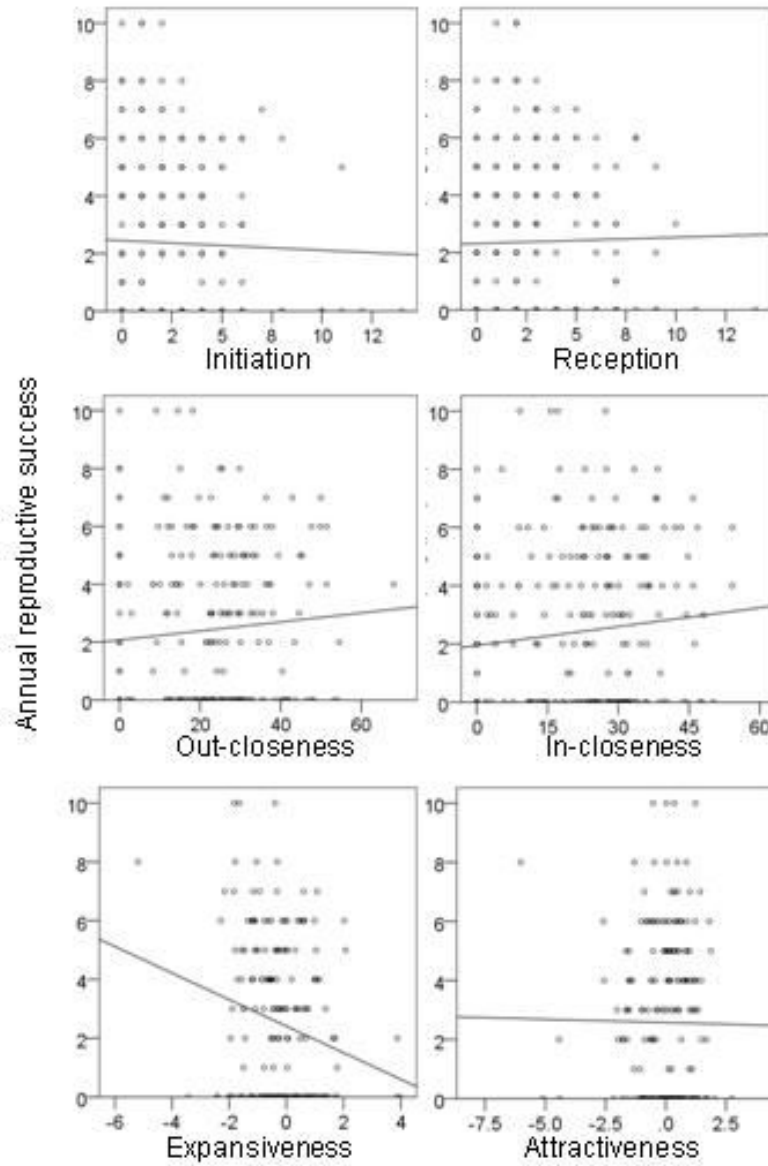
Appendix B. Null and partial model AIC values and partial model percent R^2

changes from null model. Null models included only non-social factors: year and colony for all fitness measures, and also age and sex for “Mean number of fleas”.

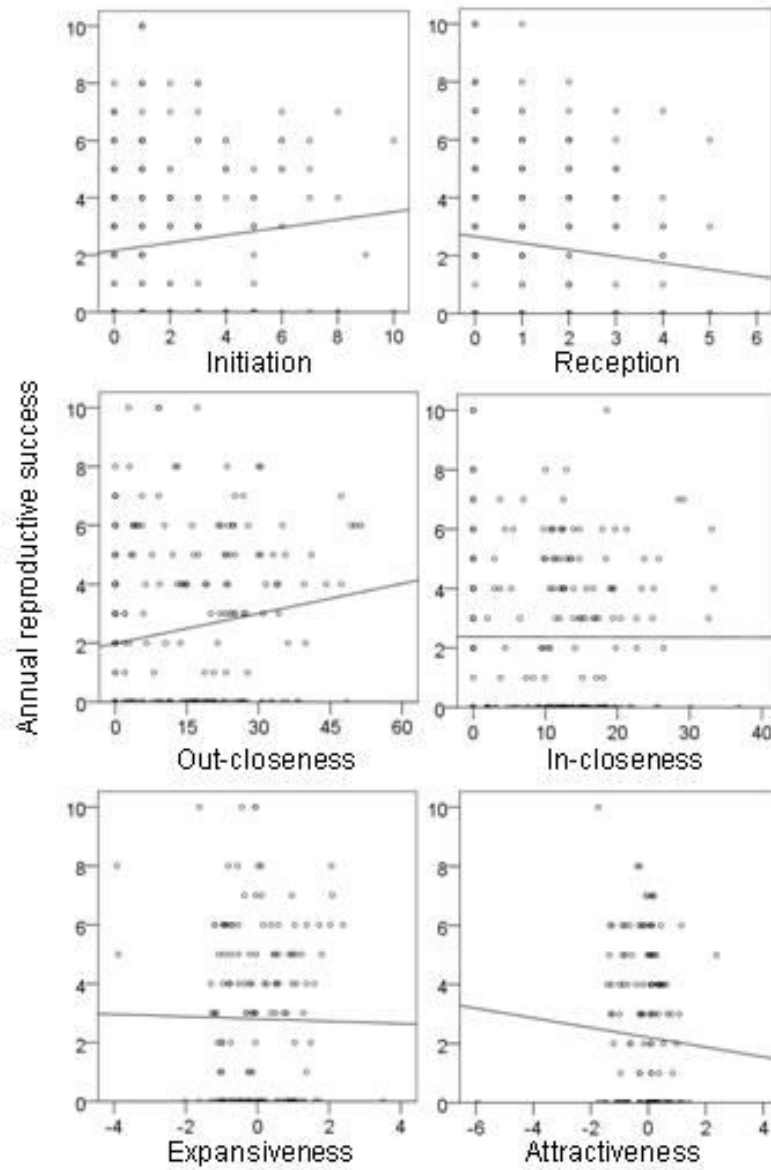
Other partial models included one additional social factor—either social group size or a social attribute. Only social attributes that were significantly associated with fitness measures and analyzed for the full dataset are presented in this table; however, social group size is presented as a comparison for social attributes, regardless of whether or not group size was significant for that fitness measure.

Fitness Measure	Age-sex Group	Partial Model for:	AIC	% Change in R^2
Number offspring	Adult females	Null	769.00	--
		Social group size	761.40	1.14
		Affiliative In-closeness	763.80	1.62
		Agonistic Initiation	764.40	1.74
		Agonistic Out-closeness	763.90	2.25
Number offspring	Adult males	Null	65.07	--
		Social group size	75.03	-0.10
		Agonistic Initiation	69.63	8.19
Mean number of fleas	All age-sex	Null	89.90	--
		Social group size	100.70	0.10
		Affiliative Initiation	95.50	2.08
		Affiliative Reception	92.47	3.43
		Affiliative In-closeness	95.27	3.52
		Agonistic Initiation	95.10	2.16
		Agonistic Out-closeness	98.57	2.03
Mean fecal GCM	Adult males	Null	13.52	--
		Social group size	24.36	-0.23
		Affiliative Out-closeness	17.13	14.30
		Affiliative In-closeness	20.83	-7.00
		Agonistic Initiation	19.93	6.89
		Agonistic Out-closeness	19.21	-3.90

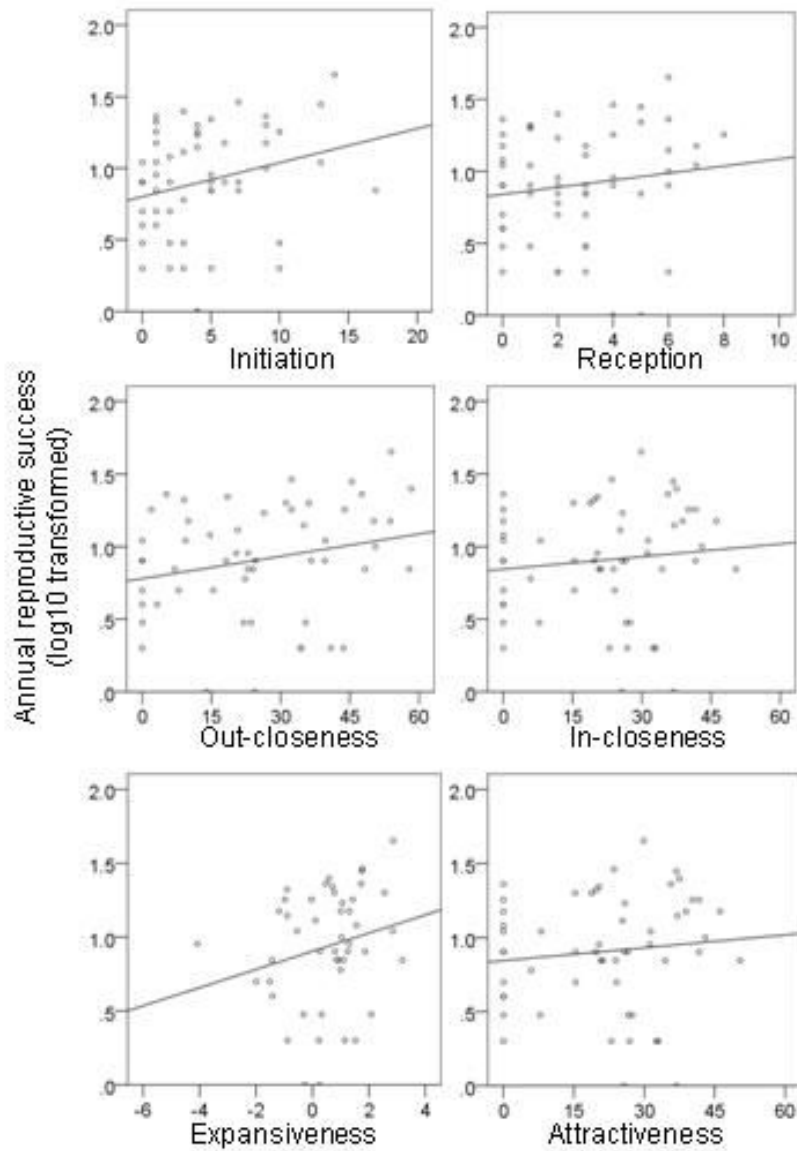
Appendix C. Annual reproductive success vs. affiliative social attributes in adult females



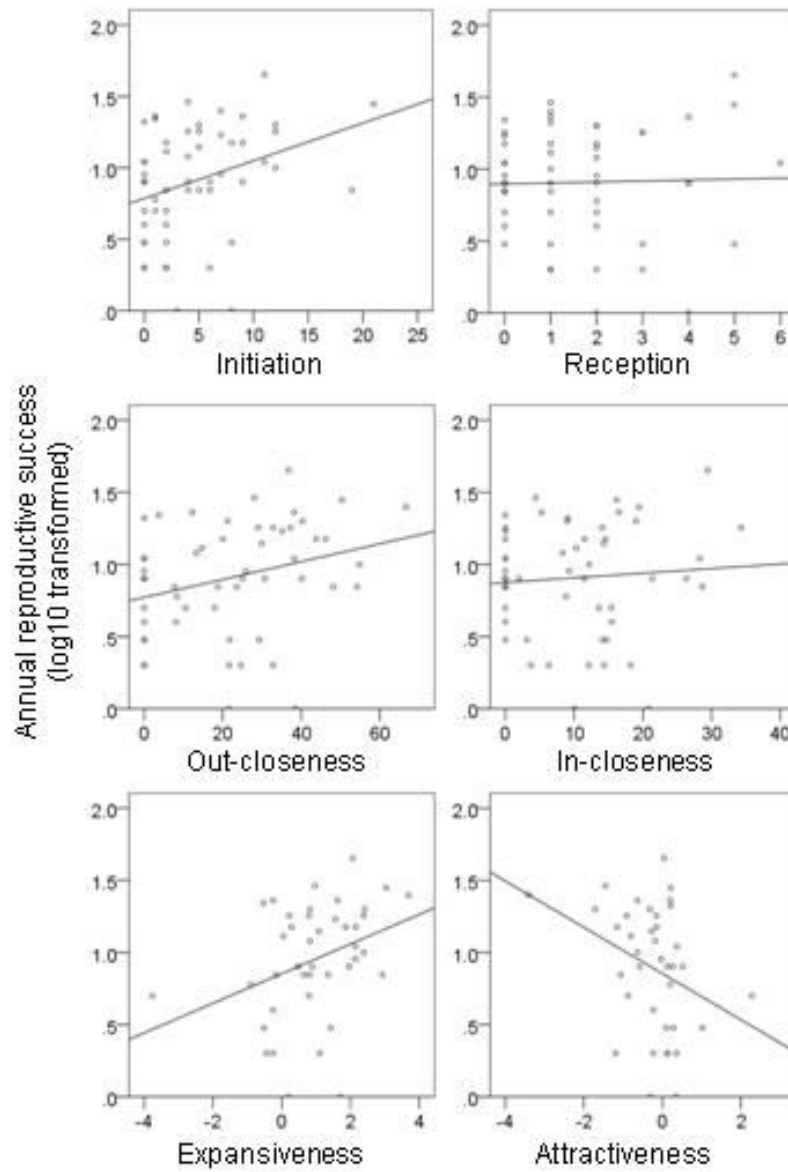
Appendix D. Annual reproductive success vs. agonistic social attributes in adult females



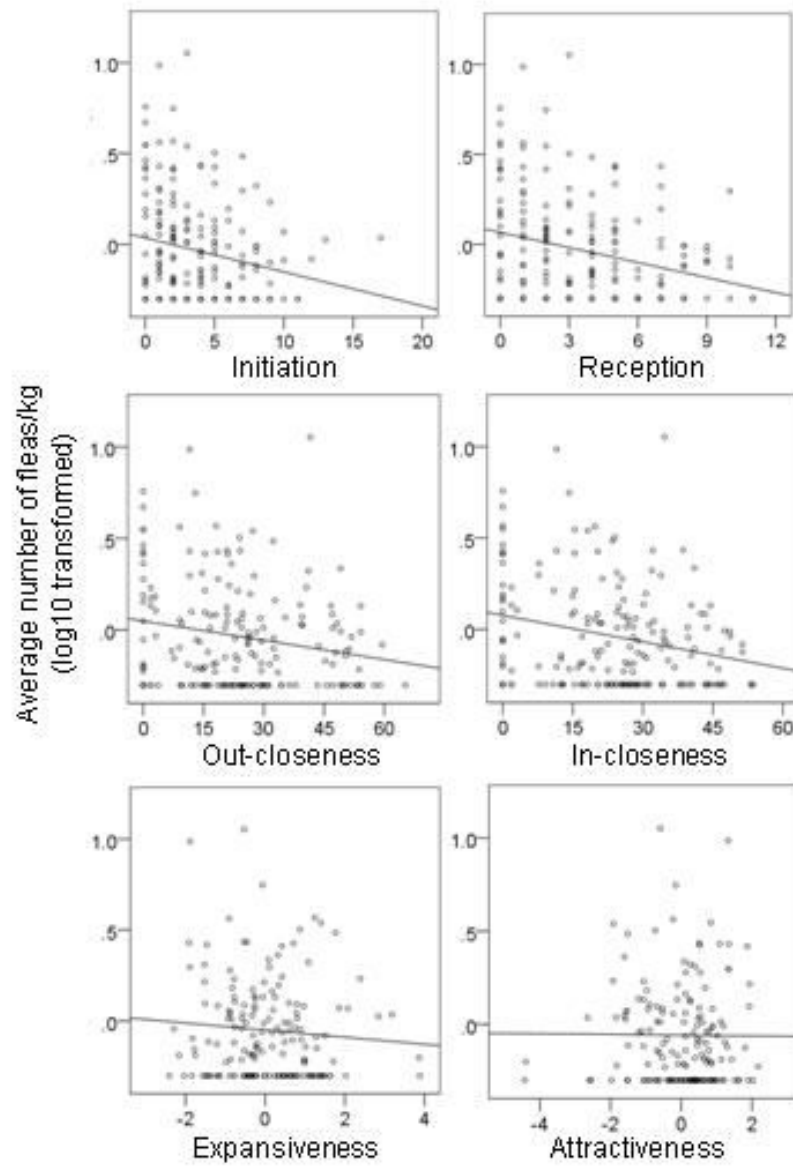
Appendix E. Log10 transformed annual reproductive success vs. affiliative social attributes in adult males



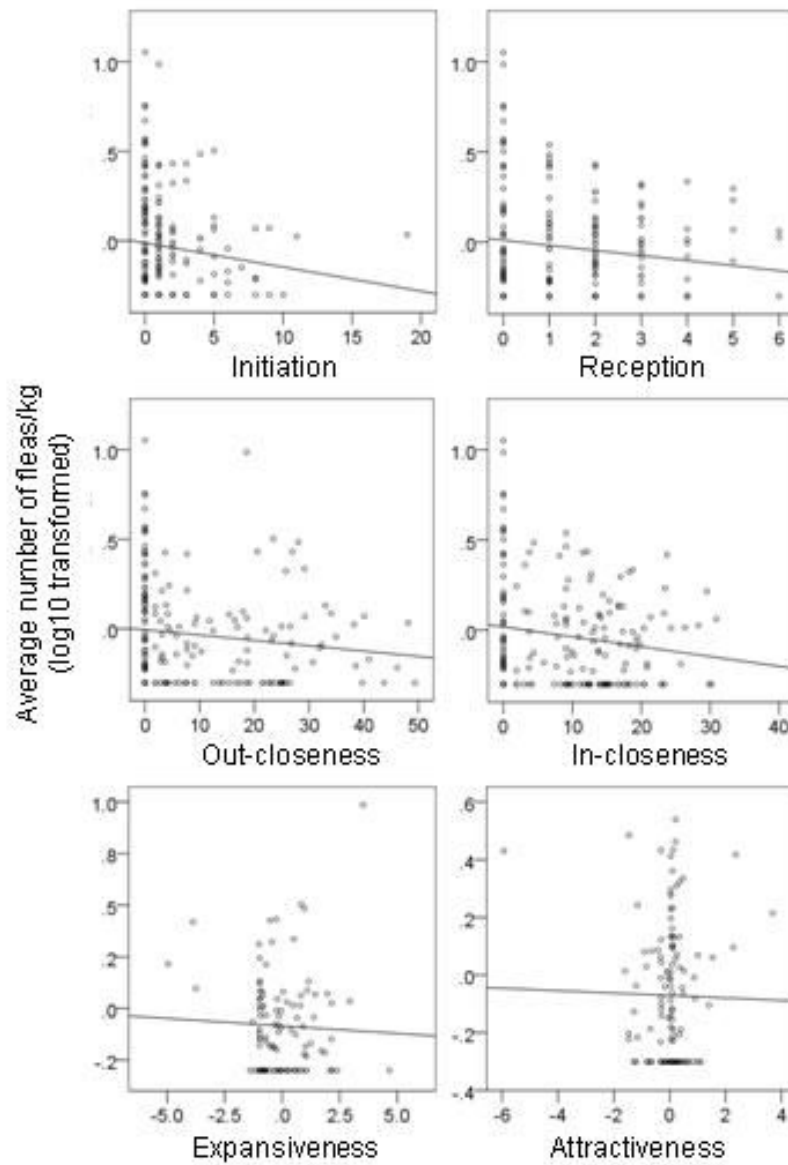
Appendix F. Log10 transformed annual reproductive success vs. agonistic social attributes in adult males



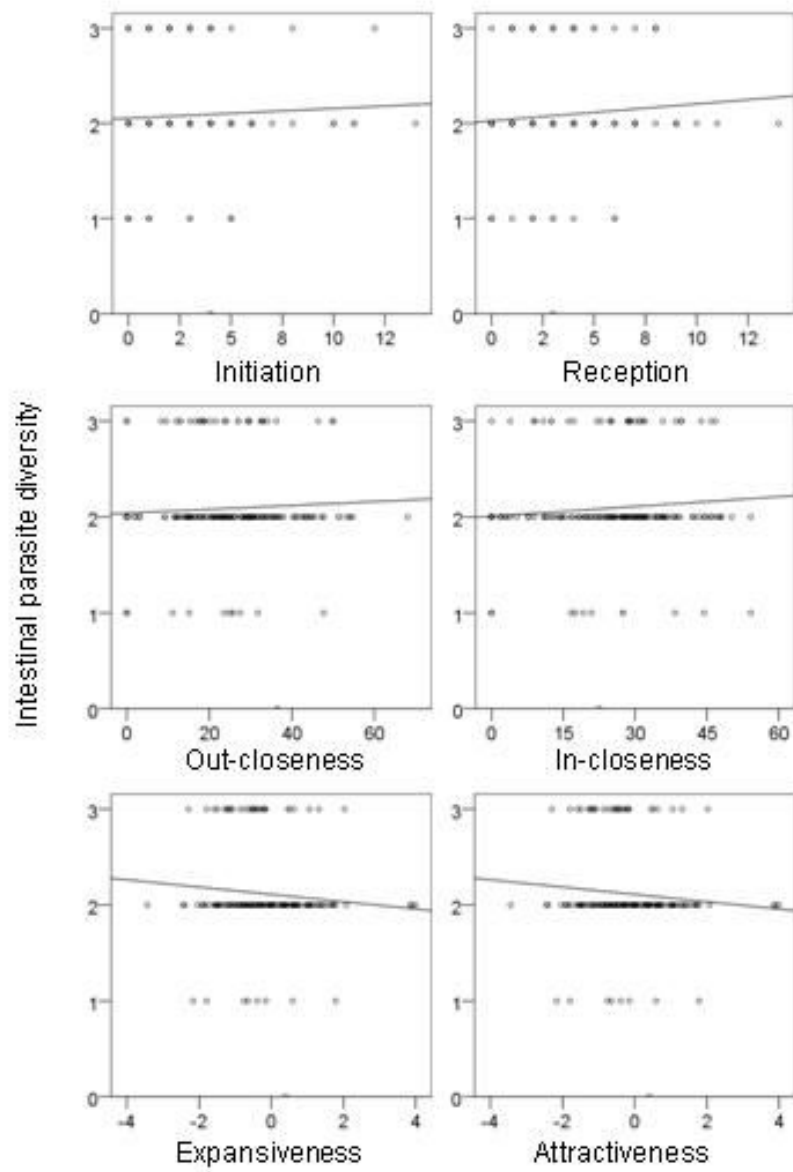
Appendix G. Log10 transformed Fleas/kg vs. affiliative social attributes for all age-sex groups combined



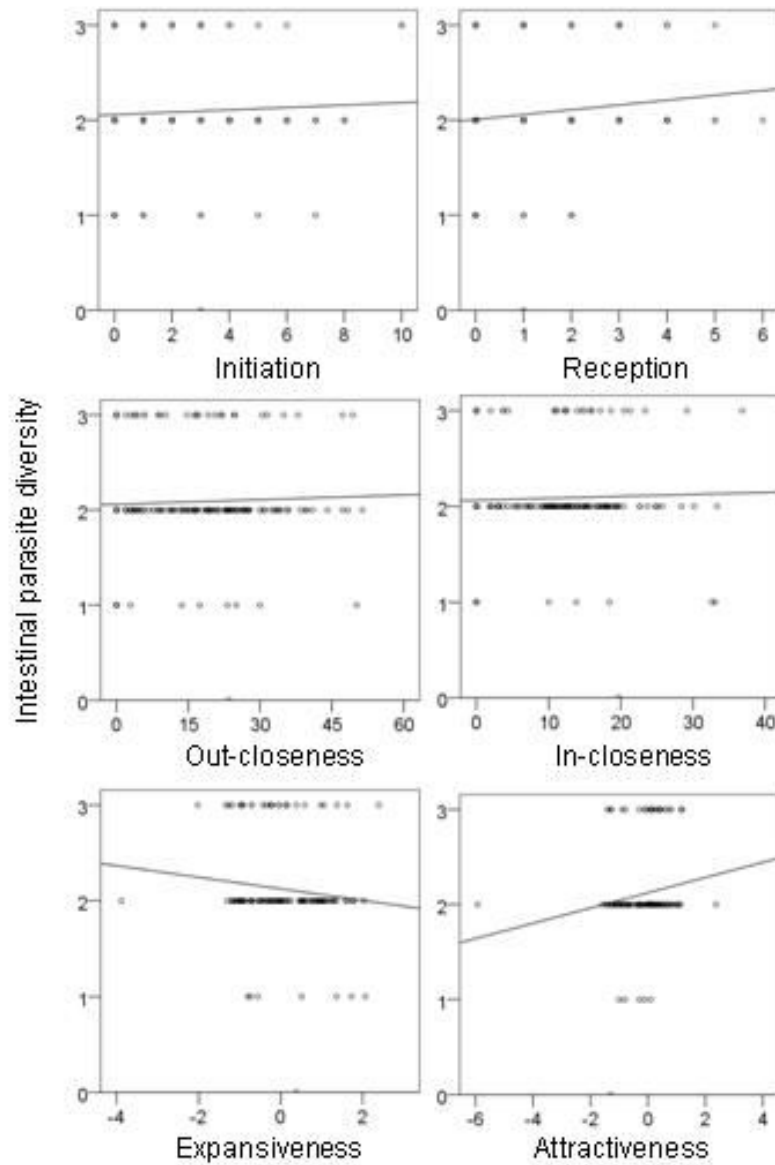
Appendix H. Log10 transformed Fleas/kg vs. agonistic social attributes for all age-sex groups combined



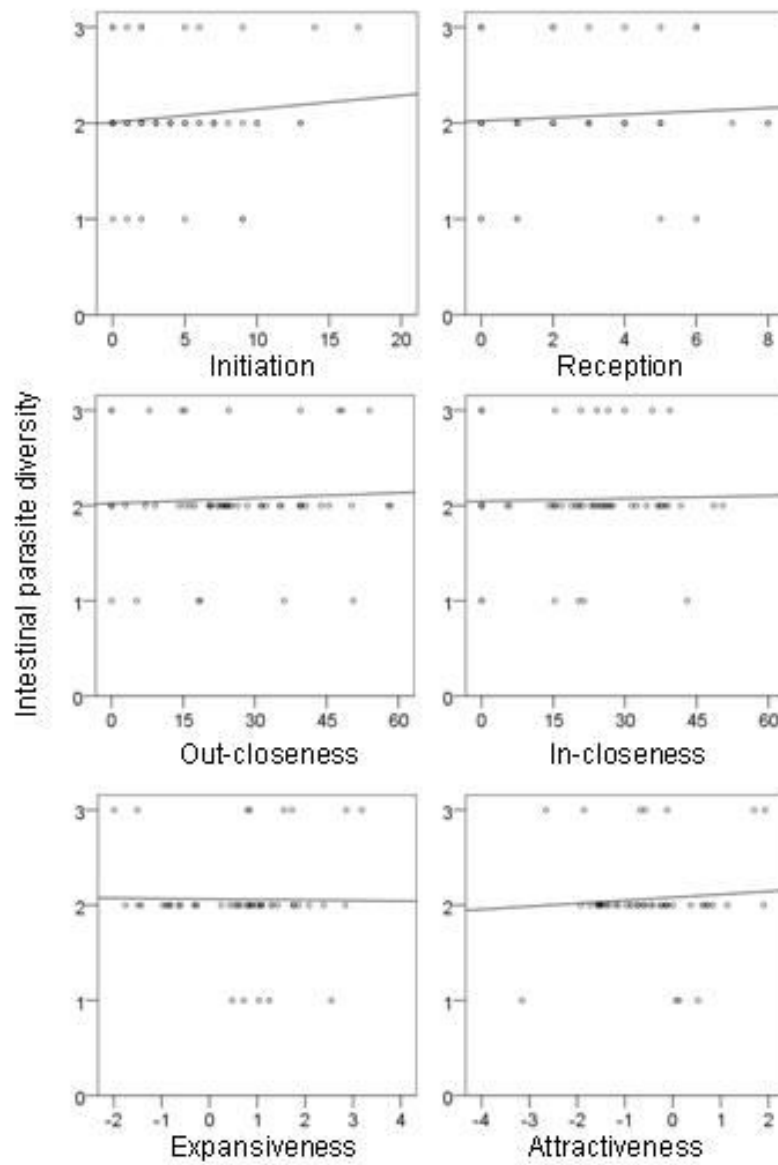
Appendix I. Gut parasite diversity vs. affiliative social attributes in adult females



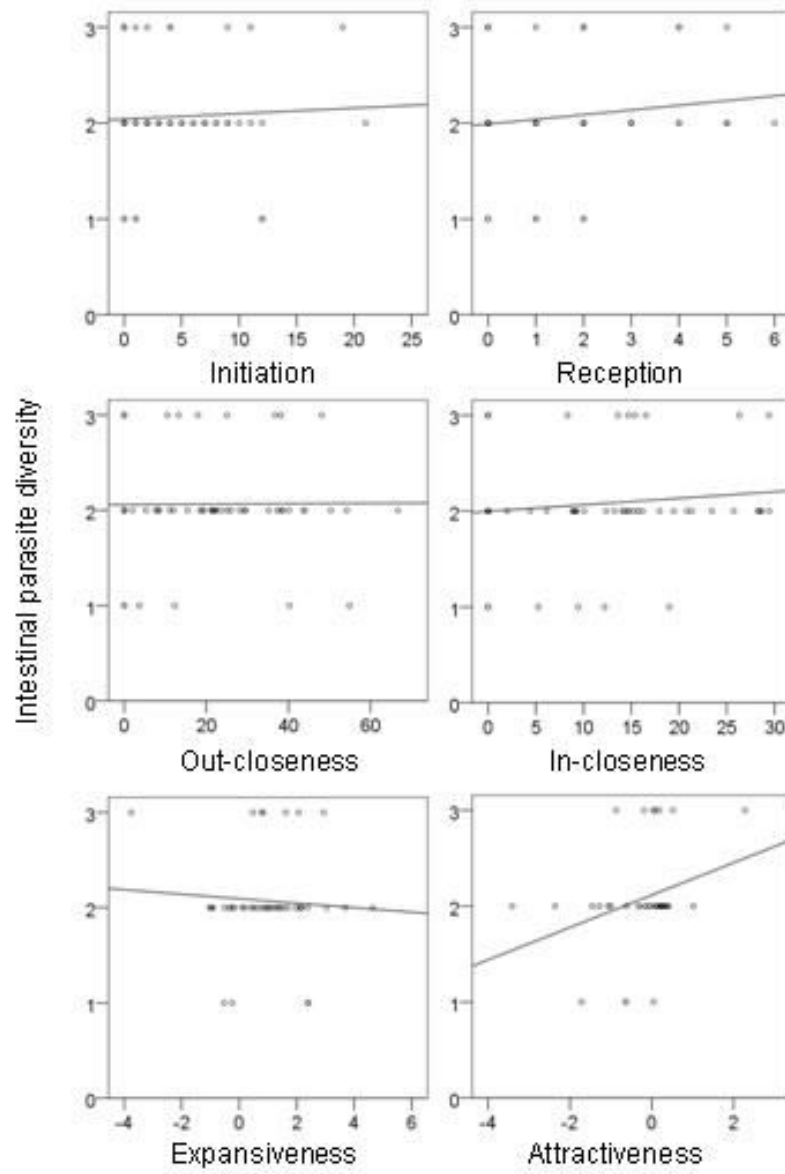
Appendix J. Gut parasite diversity vs. agonistic social attributes in adult females



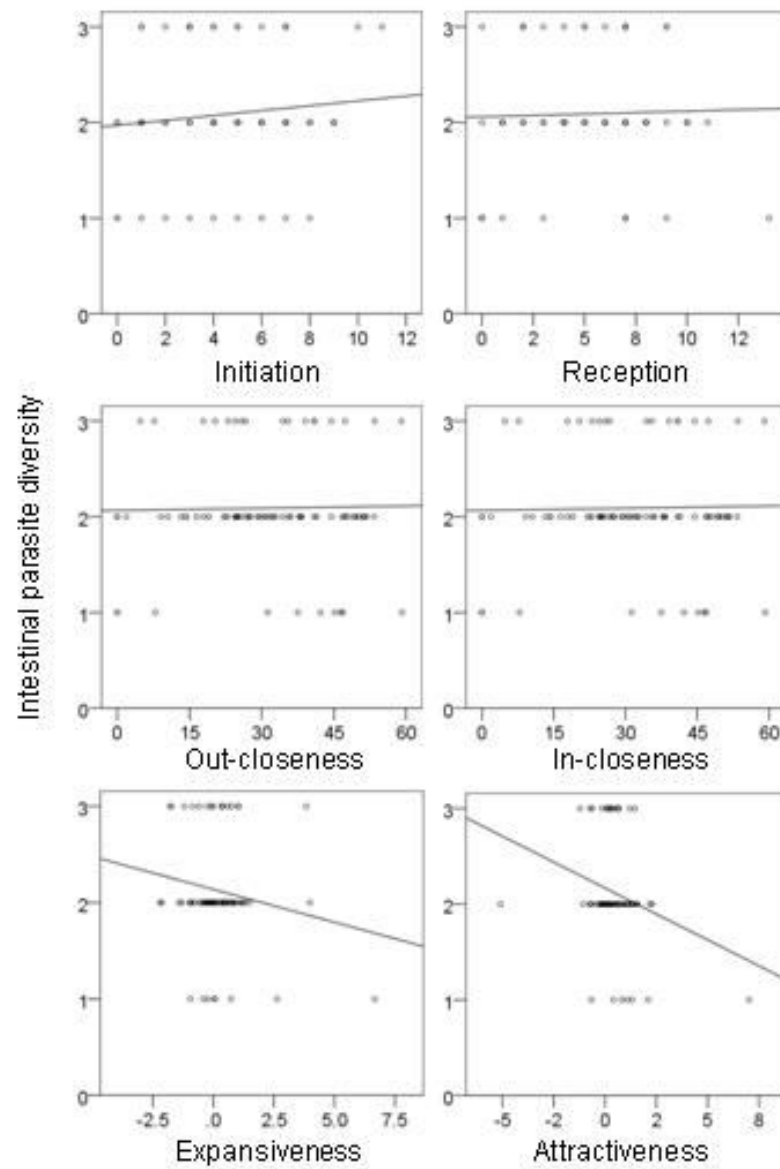
Appendix K. Gut parasite diversity vs. affiliative social attributes in adult males



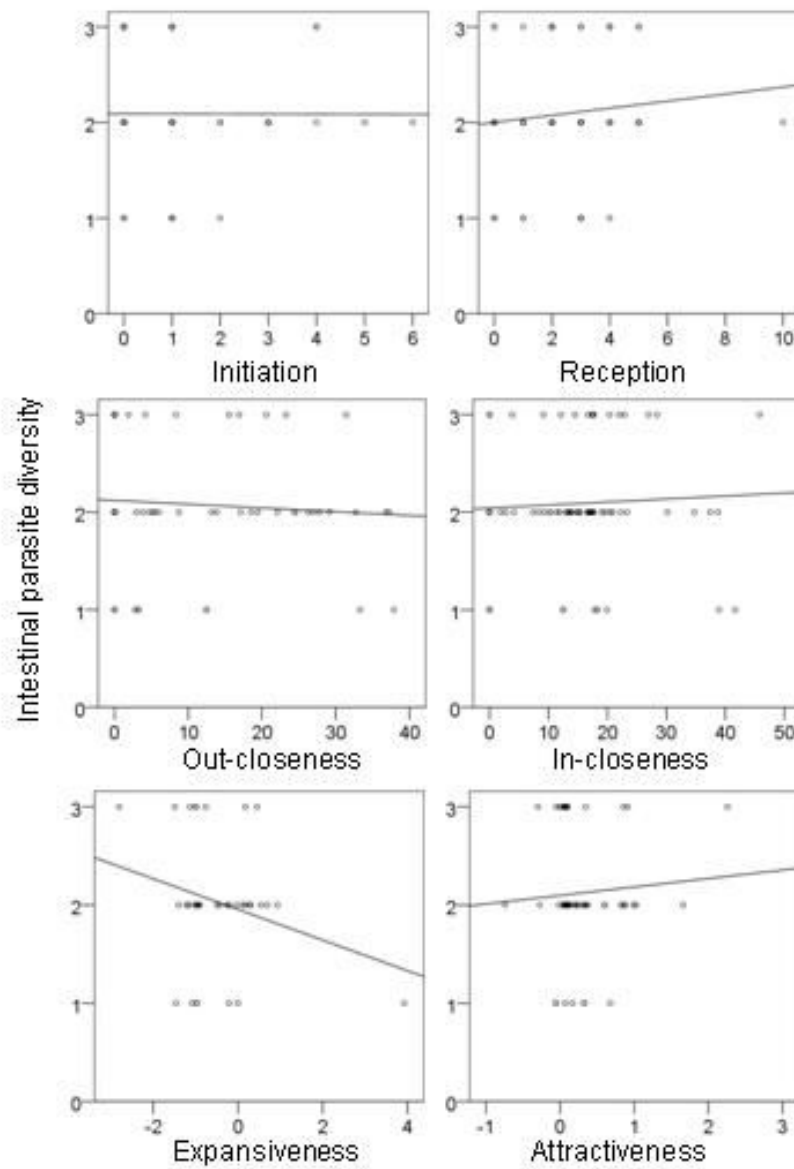
Appendix L. Gut parasite diversity vs. agonistic social attributes in adult males



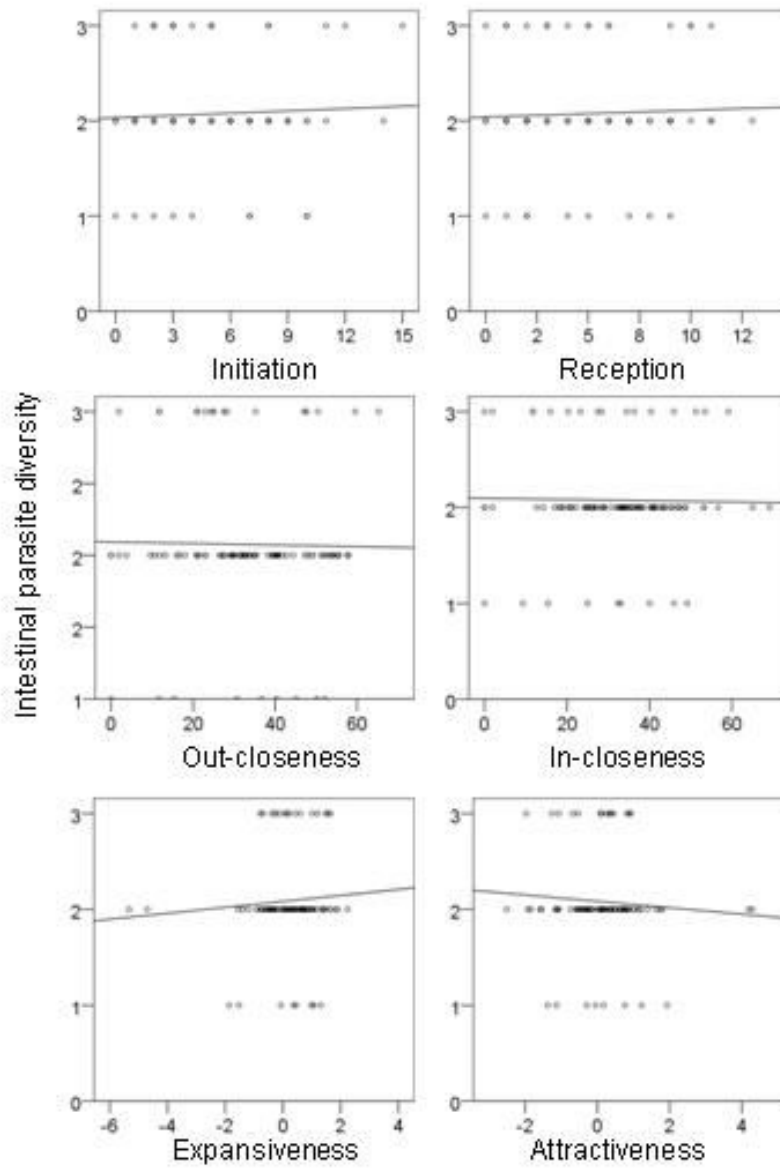
Appendix M. Gut parasite diversity vs. affiliative social attributes in yearling females



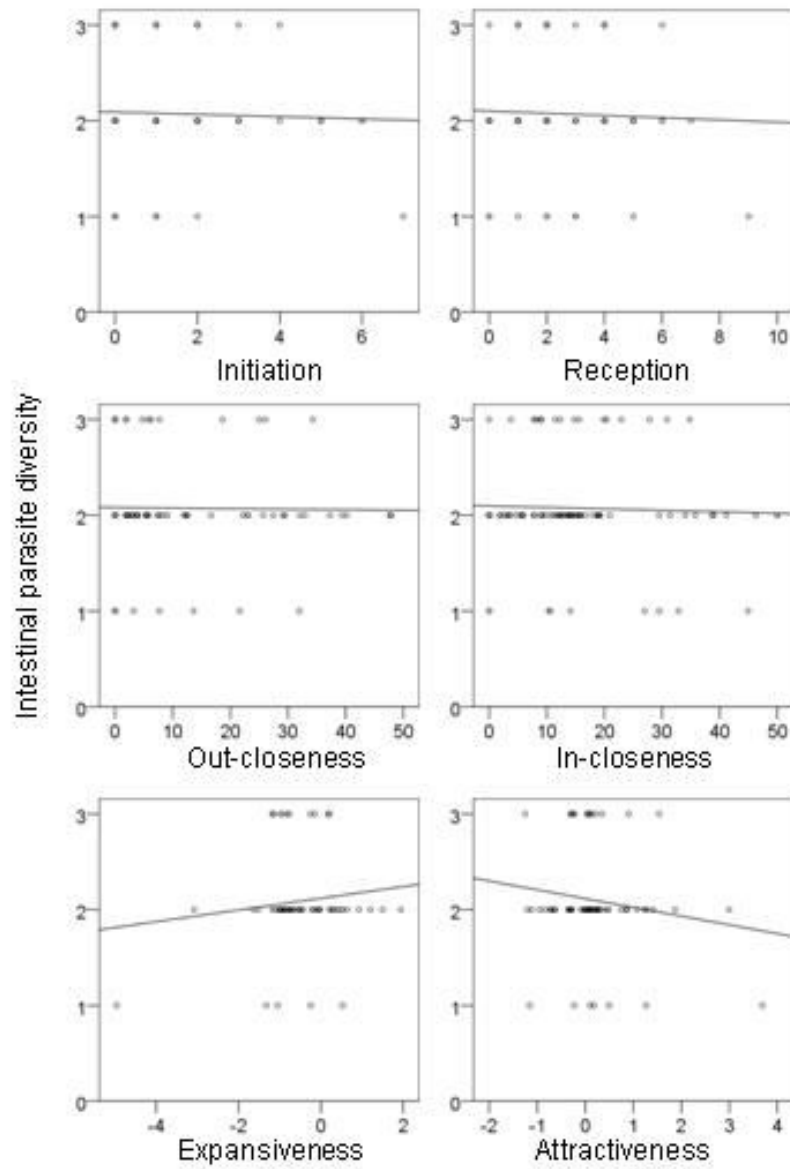
Appendix N. Gut parasite diversity vs. agonistic social attributes in yearling females



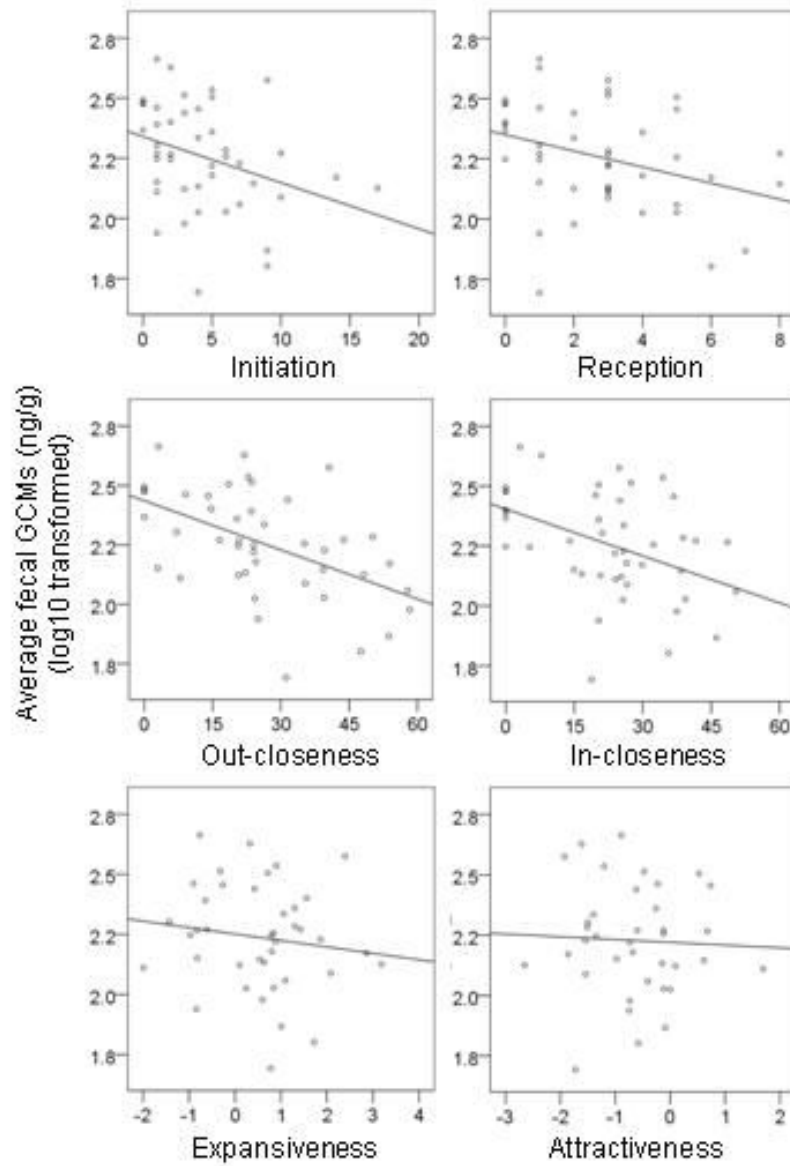
Appendix O. Gut parasite diversity vs. affiliative social attributes in yearling males



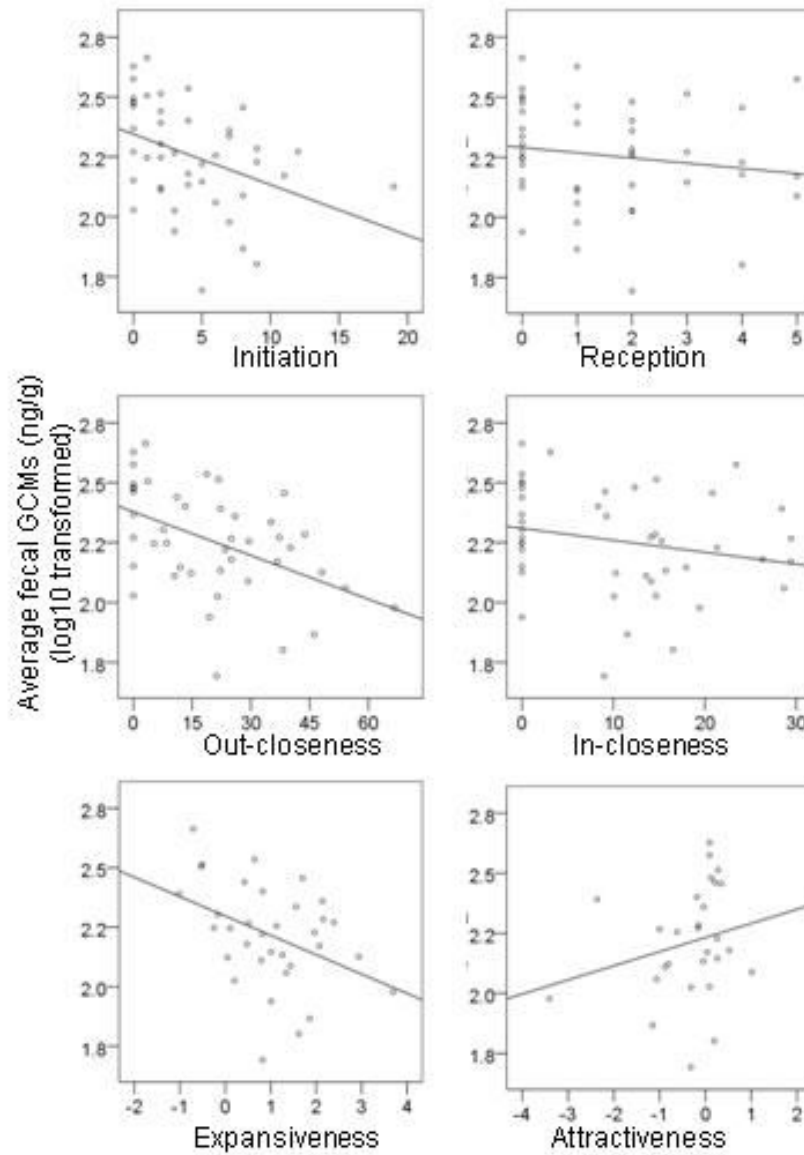
Appendix P. Gut parasite diversity vs. agonistic social attributes in yearling males



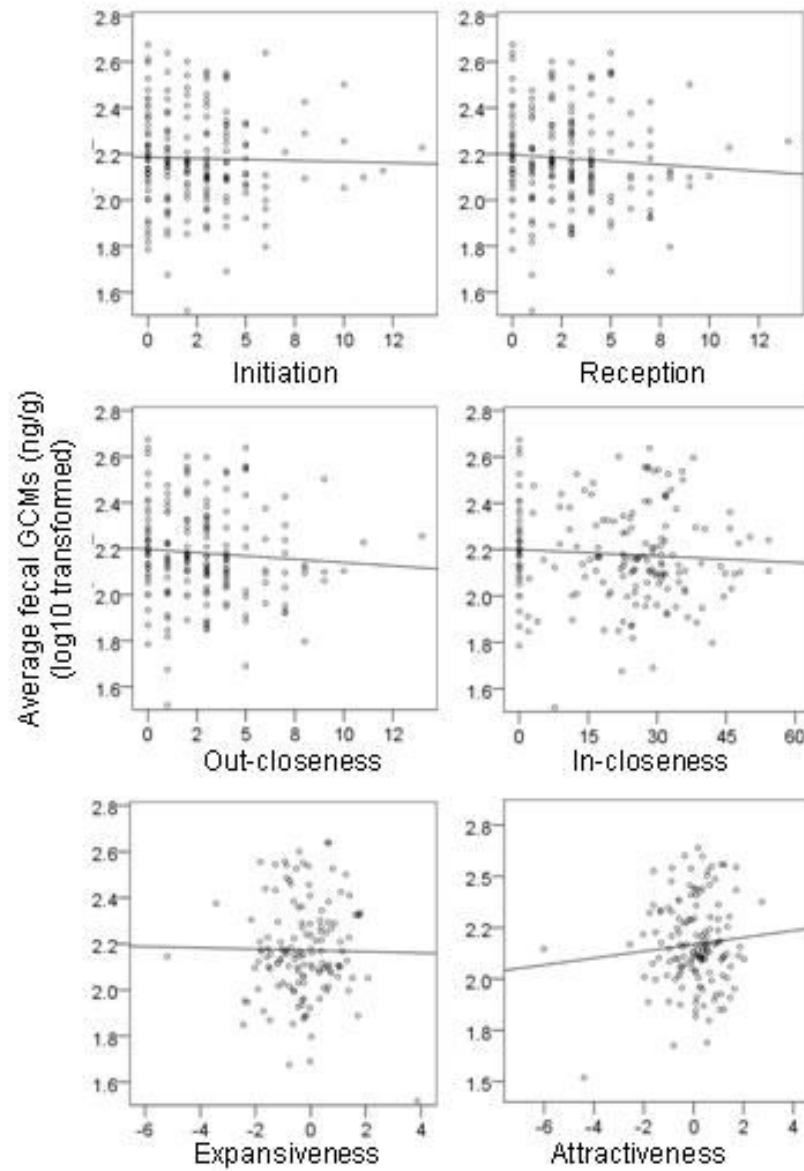
Appendix Q. Log10 transformed Fecal GCM levels vs. affiliative social attributes
in adult males



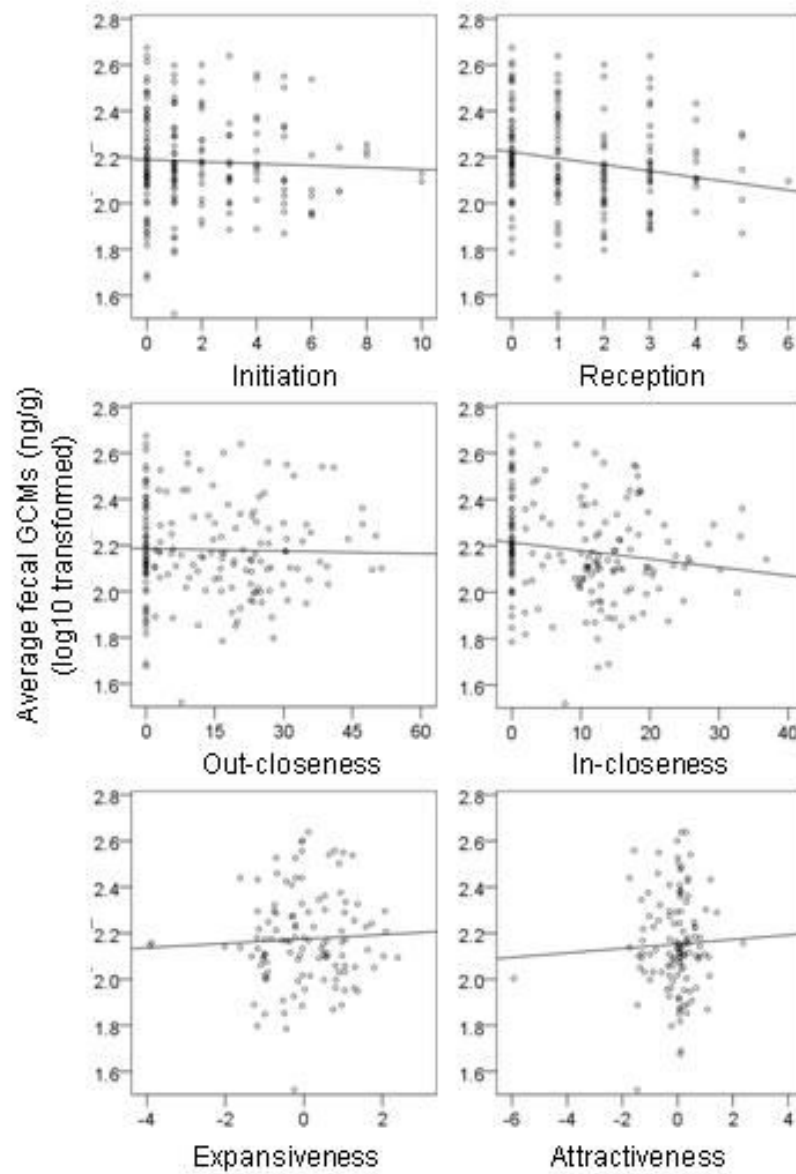
Appendix R. Log10 transformed Fecal GCM levels vs. agonistic social attributes
in adult males



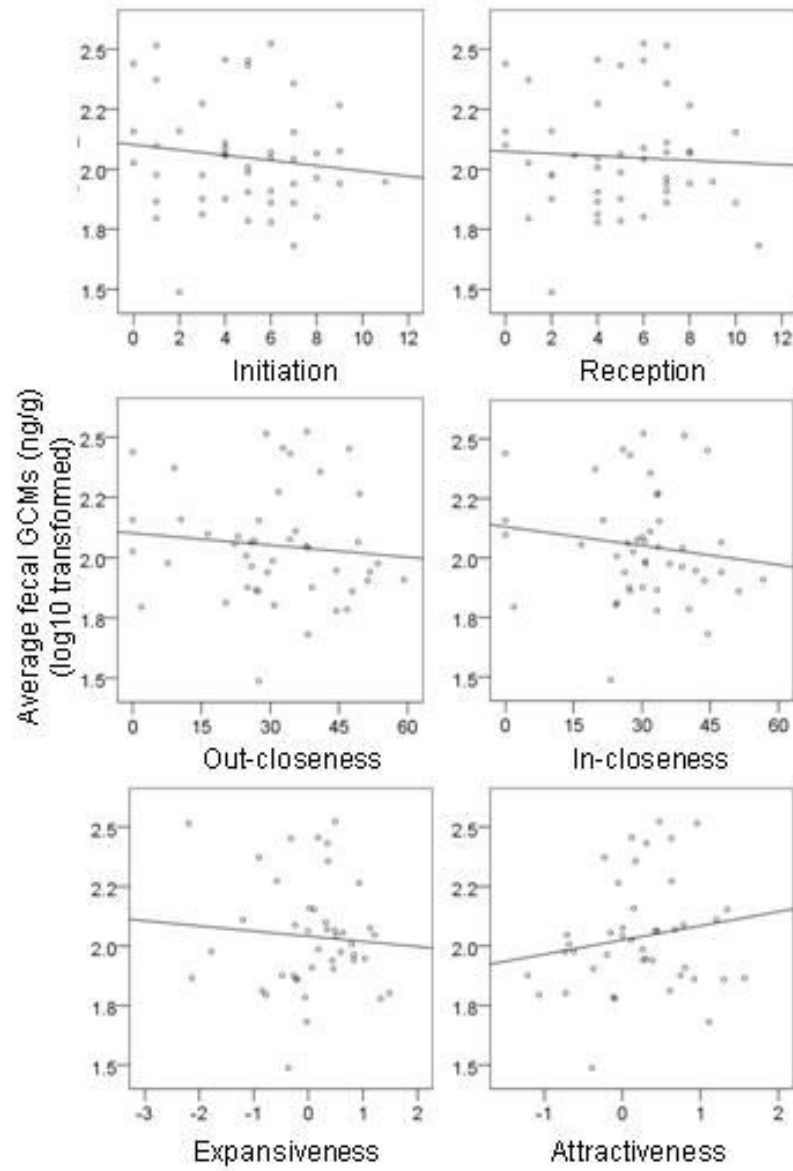
Appendix S. Log10 transformed Fecal GCM levels vs. affiliative social attributes
in adult females



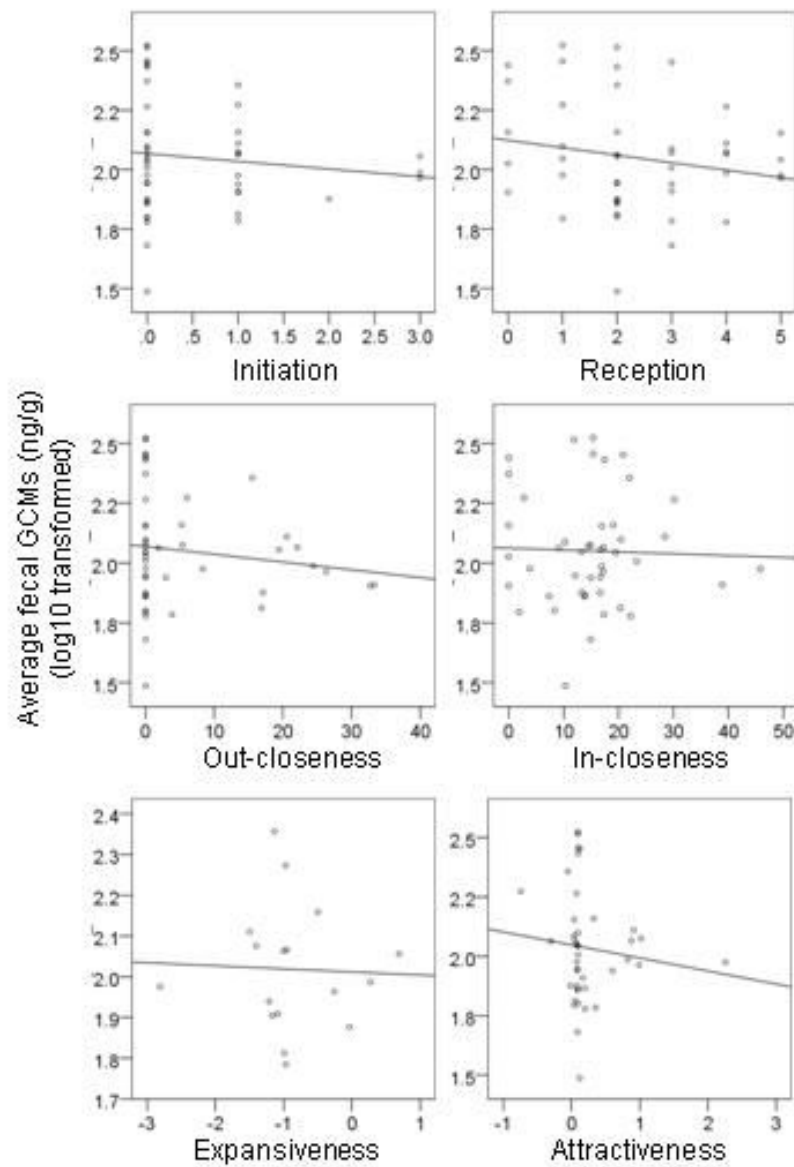
Appendix T. Log10 transformed Fecal GCM levels vs. agonistic social attributes
in adult females



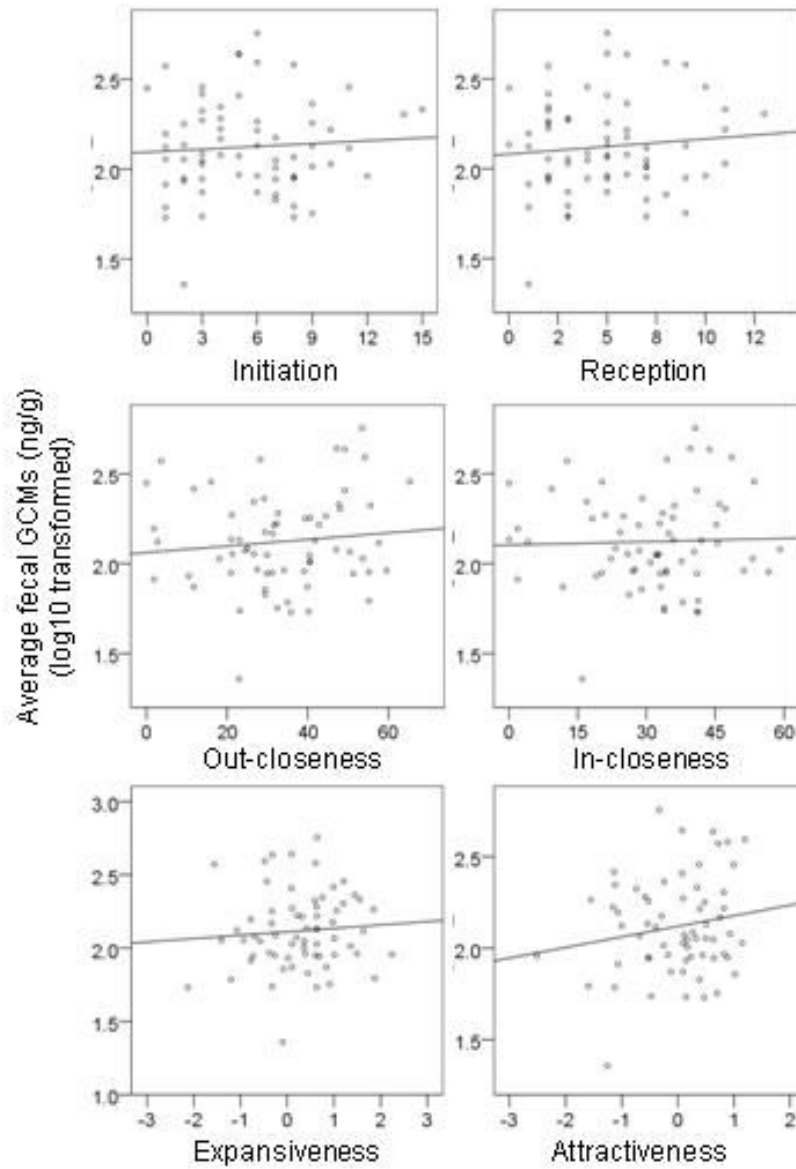
Appendix U. Log10 transformed Fecal GCM levels vs. affiliative social attributes
in yearling females



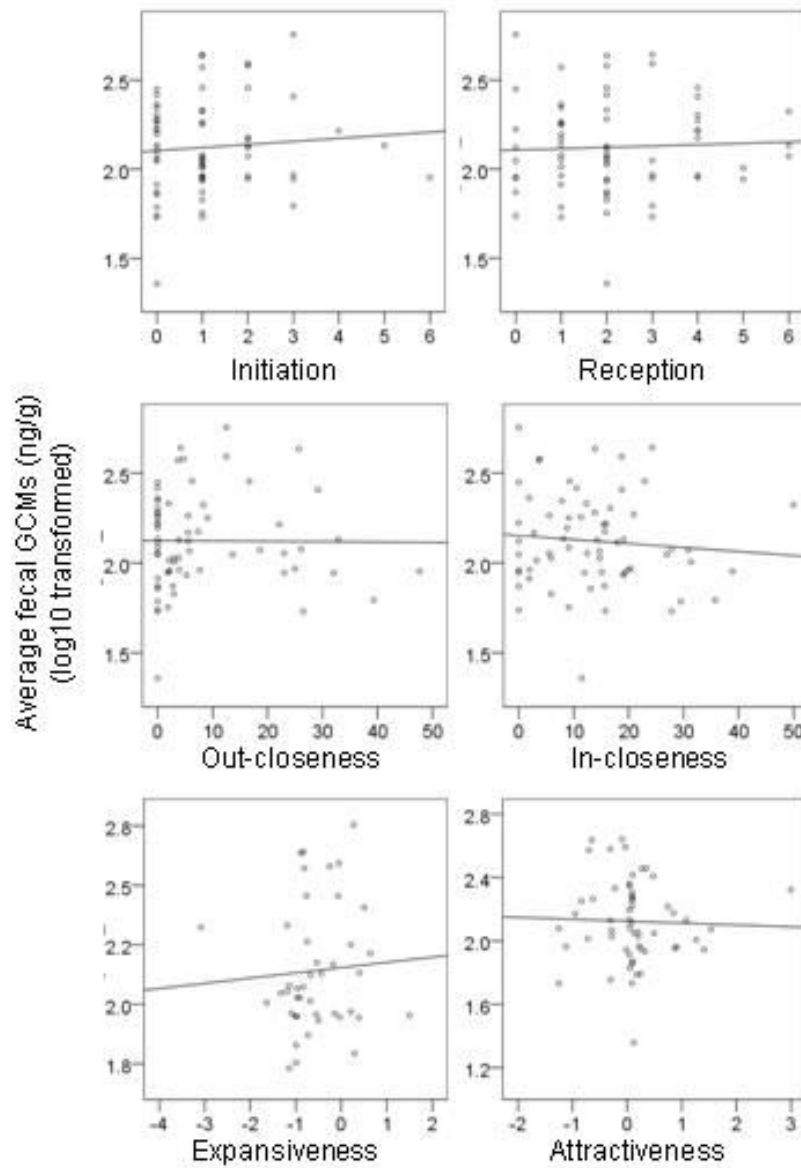
Appendix V. Log10 transformed Fecal GCM levels vs. agonistic social attributes in yearling females



Appendix W. Log10 transformed Fecal GCM levels vs. affiliative social attributes in yearling males



Appendix X. Log10 transformed Fecal GCM levels vs. agonistic social attributes
in yearling males



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