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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.

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 matrilines (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