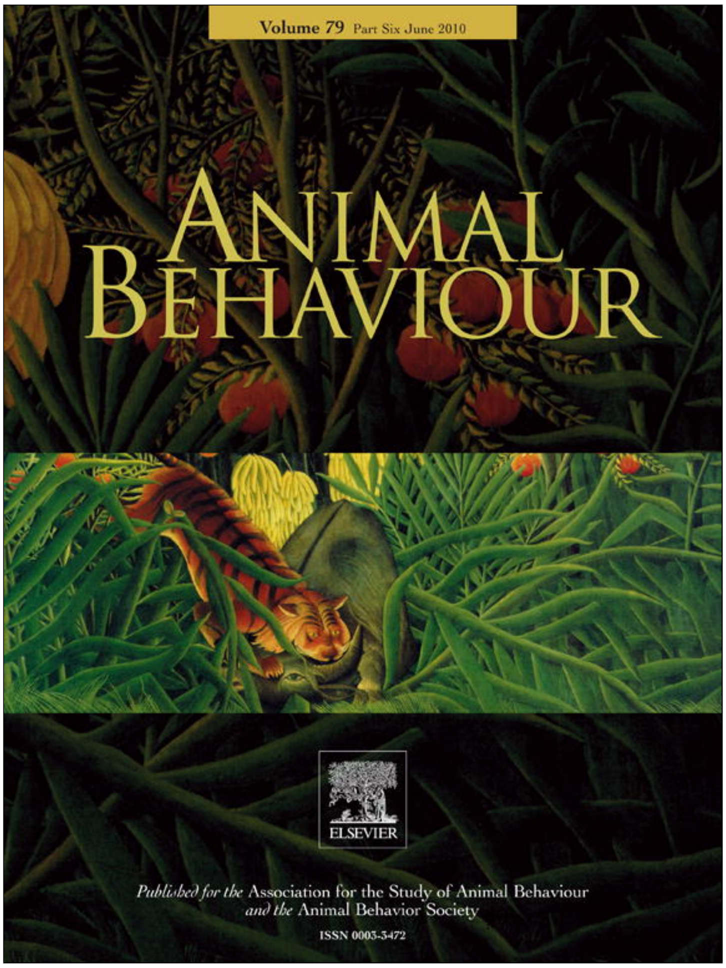
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Social cohesion in yellow-bellied marmots is established through age and kin structuring

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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

& 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 ± 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 (Konovalov 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 ± 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,

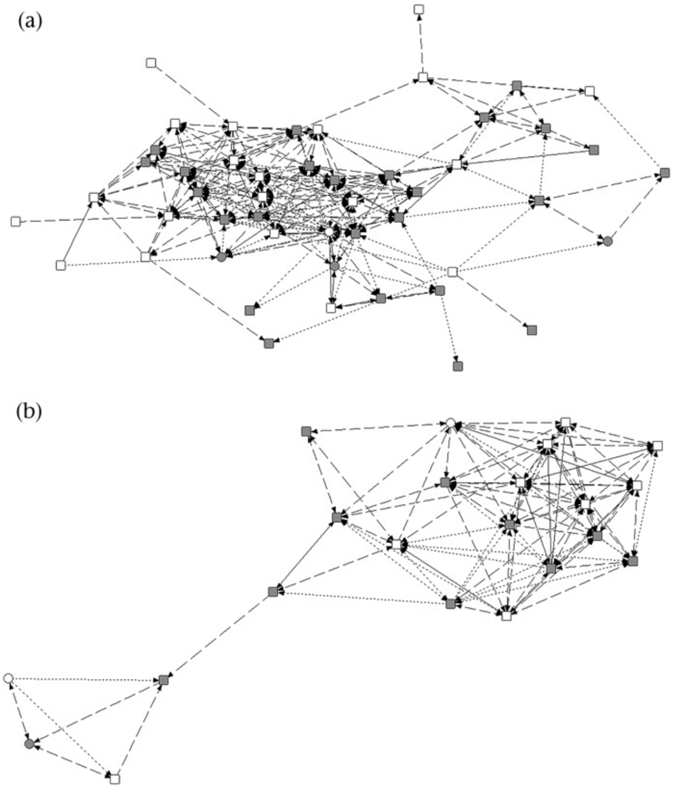

Figure 1. Two illustrative marmot social networks. (a) Picnic 2006. (b) Marmot Meadow 2007. These networks differ in size and structure. Circles: adults; squares: yearlings; grey nodes: females; white nodes: males; dashed lines: affiliative interactions; dotted lines: agonistic interactions; solid lines: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

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.

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 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
	Femal*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	Intercept	−1.055	0.323	0.001
N=276	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	
	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	
	Sex=female	−0.356	0.266	0.181
	Sex=male		0.000	
	Exact age	0.594	0.113	<0.001
	Female*exact age	−0.441	0.126	0.001
	Male*exact age		0.000	
Attractiveness	Intercept	0.191	0.211	0.367
N=376	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	
	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	
	Sex=female	0.092	0.156	0.557
	Sex=male		0.000	
	Exact age	−0.103	0.080	0.200
	Female*exact age	−0.022	0.087	0.805
	Male*exact age		0.000	
Out-closeness	Intercept	−2.476	2.504	0.323
N=276	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	
	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	
	Sex=female	0.965	1.873	0.607
	Sex=male		0.000	
	Exact age	3.903	0.878	<0.001
	Female*exact age	−1.769	0.962	0.066
	Male*exact age		0.000	
In-closeness	Intercept	8.033	2.140	<0.001
N=376	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	
	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	
	Sex=female	−0.103	1.601	0.949
	Sex=male		0.000	
	Exact age	−0.854	0.750	0.256
	Female*exact age	0.273	0.822	0.740
	Male*exact age		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	Sex		Age		Relatedness	
	P	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	Sex		Age		Relatedness	
	P	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	*P*
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	*P*
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.