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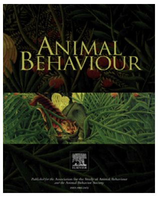

Female mountain goats, *Oreamnos americanus*, associate according to kinship and reproductive status

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In fusion–fission social systems, associations are generally weak, but animals can associate preferentially, although the ultimate and proximate causes for such associations can be multiple and depend on the species. We applied a social network approach to a population of marked female mountain goats, *Oreamnos americanus*, characterized by a fusion–fission social system in which associations between individuals are assumed to be weak. We analysed the composition of nursery groups of mountain goats from the Caw Ridge (Alberta, Canada) population from 2005 to 2008 to test whether kinship, reproductive status and differences in body mass affect associations. We hypothesized that close kin should associate more than unrelated individuals, and we expected females of similar reproductive status, age or body mass to associate more than dissimilar individuals. We used the half-weight index correcting for differences in gregariousness (HWIG) to calculate associations between dyads of females. Females did not associate at random. Immature females associated strongly with their mothers, whereas adult females associated mainly with females of similar reproductive status. Reproductive females may associate because they share similar needs during lactation. Nonreproductive adult females and females with different reproductive status associated according to their relatedness. Body mass did not influence associations between females. To our knowledge, this is the first time that a multivariate approach has been used to describe association preferences. Our results reveal how this approach can be relevant when studying the social structure of a population because it highlights the interactions between factors influencing associations.

The social structure of a population can be defined as the set of relations between individuals within groups (Hinde, 1976). It describes the relations (i.e. associations and/or interactions) between individuals living near each other (Whitehead, 1997). Therefore, repeated interactions between individuals within a group can lead, for example, to the development of cooperative relations, dominance hierarchy or cultural transmission (Croft et al., 2006; Gilby & Wrangham, 2008; Wey, Blumstein, Shen, & Jordán, 2008). Social structure may also influence the biology of individuals or populations, for example by affecting individual fitness, gene flow or spatial distribution (Whitehead, 1997). In addition, the rate of transmission of information or diseases depends on the social structure of a population (Fenner, Godfrey, & Bull, 2011; Hamede, Bashford, McCallum, & Jones, 2009; Voelkl & Noë, 2008; Wey et al., 2008).

The social network approach is a powerful tool to describe the social structure of a population, specifically to examine why and how individuals associate. When groups are fluid, such as in species characterized by a fusion–fission system (Kummer, 1971), the mechanisms of association are not fully understood, although recent studies have shown that in taxa as diverse as fishes, dolphins and zebras, the social structure is nonrandom and highly structured (Croft et al., 2005; Lusseau et al., 2003; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007). In fusion–fission social systems, associations are generally weak, but animals can associate preferentially. For example, the benefit–cost ratio of living in groups may be higher for kin than for nonkin, and kin selection may have led to the evolution of stronger associations between kin than between nonkin (Hamilton, 1964a, 1964b). African elephants, *Loxodonta africana*, form matriarchal societies in which group fusion and fission are influenced by genetic relatedness: during fission events females remain with their first-order maternal relatives, and fusions are most likely occur between groups whose matriarchs are genetically related (Archie, Moss, & Alberts, 2006). In other species

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such as the striped dolphin, *Stenella coeruleoalba* (Gaspari, Zillion, Airoldi, & Hoelzel, 2007) and the red deer, *Cervus elaphus* (Albon, Staines, Guinness, & Clutton-Brock, 1992), females form groups according to their relatedness. Association between close kin may be favoured when the level of aggressive interactions among individuals is high. Galapagos sea lions, *Zalophus wollebaeki*, for example, are aggressive and also show a higher tolerance for genetically similar individuals (Wolf & Trillmich, 2008). Female mountain goats show very high levels of aggressiveness relative to other ungulates (Côté, 2000) and, as in sea lions, females may show higher tolerance towards their close kin than towards unrelated individuals.

Other factors than kin selection may explain nonrandom associations. Differences in body size between sexes could create differences in time budgets, which may in turn affect the synchronization of individuals and prevent them from forming cohesive groups (Ruckstuhl, 1998, 1999). Differences in body mass and size can also explain why individuals sometimes segregate by age (Ruckstuhl, 2007). Croft et al. (2005) showed that guppies, *Poecilia reticulata*, interacted more with individuals of similar body length than with other individuals. Reproductive status could also influence female associations and group formation. In ungulates, lactating females forage longer than nonlactating females (Hamel & Côté, 2008; Ruckstuhl & Neuhaus, 2002). Therefore, segregation of females of different reproductive status may result from a lack of synchronization generated by different time budgets. Moreover, lactating females sometimes select different habitats than nonlactating females, which can lead to segregation (Stone's sheep, *Ovis dalli stonei* Allen 1897: Walker, Parker, & Gillingham, 2006; caribou, *Rangifer tarandus*: Barten, Bowyer, & Jenkins, 2001).

We used a long-term data set on group composition in the Caw Ridge (AB, Canada) mountain goat population to examine whether females show nonrandom associations and to determine which factors could affect preferences in their associations, if any. We investigated the role of relatedness, reproductive status, age and body mass differences on association patterns. We first determined whether the social structure of females was random or not. We then studied associations between dyads of females based on group membership (Lusseau, 2003; Sundaresan et al., 2007). Although female mountain goats do not seem to show any strong long-term kin associations, some females have been seen in associations with their daughters for up to several years (Festa-Bianchet & Côté, 2008). We hypothesized that the social network of mountain goats is affected by relatedness between individuals: we expected that females would associate preferentially with close relatives. In addition, we expected that reproductive status and differences in age and body mass between females would affect their association patterns: associations between similar individuals should be stronger than associations between dissimilar individuals. To analyse the social network of mountain goats we applied a random effect regression tree analysis, a multivariate method that also permitted us to test interactions between variables.

METHODS

Study Species

The study was conducted at Caw Ridge (54°N, 119°W), west-central Alberta, in the Canadian Rocky Mountains, between 1750 m and 2170 m in elevation. The area used by the unhunted native mountain goat population is about 28 km^2. Population size increased from 94 individuals in 1989 to 149 individuals in 2008 (Festa-Bianchet & Côté, 2008). Goats are captured from late May to mid-September each year in box traps. Individuals are weighed at capture without being handled using electronic platform scales baited with salt (Bassano, von Hardenberg, Pelletier, & Gobbi, 2003). Individuals 3 years and older are chemically immobilized during capture. Kids have not been captured since 1998 because of a high risk of abandonment (Côté, Festa-Bianchet, & Fournier, 1998). Since 1993, 98% of individuals older than 1 year (100% of females) have been marked, and their age known. Ear tissue samples have been taken for DNA analysis to confirm the relationship between a kid and its mother that was first determined in the field from visual observations (Mainguy, Côté, & Coltman, 2009). Females generally produce their first kid at the age of 4 or 5 years, and produce one kid annually, although reproductive pauses are common (Côté & Festa-Bianchet, 2001). The intraspecific aggression rate in female mountain goats is the highest ever measured in nature for female ungulates (Fournier & Festa-Bianchet, 1995). Groups of goats are easily observable and are defined as associations of individuals whose nearest neighbour is at a maximum distance of 100 m. Females form small groups in early June, after giving birth; group sizes increase during the season until they reach their maximum size in the middle of summer, where almost all the females of the population may form one large group (Festa-Bianchet & Côté, 2008). We searched the whole area on a daily basis. Almost all the goats were observed every day, for the whole day. The groups are not permanent and may change every day. Almost all the study area is searched daily for goats. Groups are noted and their members are identified each day between mid-May and mid-September using spotting scopes (15–45×) at distances ranging from 200 to 700 m (Festa-Bianchet & Côté, 2008). Adult males very rarely overlap with females during summer and, thus, were not included in the analyses.

Structure of the Social Network of Female Mountain Goats

We studied associations between females that were at least 1 year old. Kids were not considered because they were always associated with their mothers (Festa-Bianchet & Côté, 2008). We used group composition data from 2005 to 2008 to build one network per year because the mean number of observed associations per dyad was large enough to obtain representative patterns of social relationships for each year (Whitehead, 2008). Group observations were carried out from mid-May to mid-September each year. We only considered for the analyses groups in which all individuals were identified (427 groups in 2005, 394 in 2006, 282 in 2007 and 335 in 2008; Chilvers & Corkeron, 2002; Lusseau et al., 2003). Two animals were considered associated if they were seen in the same group.

To estimate the association between two individuals ‘a’ and ‘b’, we first calculated the half-weight index (HWI):

$$\mathrm{HWI}_{\mathrm{ab}} = x \Big/ \left({}^{1}\!/\!{}_{2}\,(n_{\mathrm{a}} + n_{\mathrm{b}}) \right) \tag{1}$$

where x is the number of times that individuals a and b were seen in the same group; n_{a} and n_{b} are the total number of times that individuals a and b were seen (Whitehead, 2008). Because gregariousness (defined as mean group size experienced by an individual) varied considerably during summer, between individuals during a summer, and between years (mean ± SE group size for 2005: 42 ± 7; 2006: 30 ± 5; 2007: 55 ± 12; 2008: 54 ± 12), we also used a new association index (HWIG) derived from the half-weight index (HWI) but correcting for the bias caused by gregariousness (Godde, Humbert, Côté, Réale, & Whitehead, 2013):

$$\mathrm{HWIG}_{\mathrm{ab}} = \mathrm{HWI}_{\mathrm{ab}} \Big/ \left(\sum \mathrm{HWI}_{\mathrm{a}} \times \sum \mathrm{HWI}_{\mathrm{b}} \Big/ \sum \mathrm{HWI} \right) \tag{2}$$