



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.

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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, Airoidi, & 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 wolfebaeki*, 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 un hunted native mountain goat population is about 28 km². 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):

$$HWI_{ab} = x / \left(\frac{1}{2} (n_a + n_b) \right) \quad (1)$$

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 \pm SE group size for 2005: 42 \pm 7; 2006: 30 \pm 5; 2007: 55 \pm 12; 2008: 54 \pm 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):

$$HWIG_{ab} = HWI_{ab} / \left(\sum HWI_a \times \sum HWI_b / \sum HWI \right) \quad (2)$$

where HWI_{ab} and $HWIG_{ab}$ are the half-weight index and the half-weight index corrected for gregariousness for the pair of individuals a and b, respectively. $\sum HWI_a$ and $\sum HWI_b$ represent the sum of all half-weight indices for individuals a and b, including all individuals in the population, respectively. $\sum HWI_a$ is a measure of the gregariousness of individual a. $\sum HWI$ is the sum of half-weight indices for all dyads of the population (i.e. a measure of the gregariousness of the whole population). HWIG is the calculated half-weight index divided by its expected value if individuals associated at random but based on their own calculated gregariousness. The association between two individuals is considered as random when $HWIG = 1$; if HWIG is <1 , then the two individuals avoid each other; if HWIG is >1 , then the two individuals prefer each other (Godde et al., 2013). HWIG has the advantage of being more robust than HWI to biases caused by individual gregariousness. To obtain an unbiased estimation of the gregariousness of a female, we calculated HWIGs by including all individuals. We then removed young males present in the nursery groups and females that were seen less than 15 times for the following analyses. We used weighted networks rather than binary networks (Franks, Ruxton, & James, 2010; Whitehead, 2009), considering HWIG as a measure of the strength of the association between two individuals.

For each year, we used Monte Carlo permutation tests (Bejder, Fletcher, & Bräger, 1998) modified by Whitehead, Bejder, and Ottensmeyer (2005) to test for the randomness of the network. By permuting associations within samples we corrected for gregariousness, consequently for this analysis HWI was used instead of HWIG. Other factors such as demographic aspects (e.g. dispersion or death of individuals during the study period) were also taken into consideration by the permutation tests. As recommended by Whitehead et al. (2005), each observed association matrix (one per year between 2005 and 2008) was randomized 25 000 times using 1000 flips per permutation. We compared the standard deviation of the observed association indices versus randomized ones to test (two-tailed test) the null hypothesis that the network structure of females (each year) was random.

Factors Influencing the Strength of Female Associations

The same dyads were present during several years. Moreover, association data were not independent within years because transitivity could occur. For example, individuals a and b were often in the same groups and so were individuals a and c. As a consequence, individuals b and c were also often in the same groups. Thus, using HWIGs, we constructed two regression trees (De'ath, 2002) with random effects (EM algorithm: Sela & Simonoff, 2009), the first including all females, the second one including only sexually mature females ≥ 3 years old. We carried out this second test to verify whether mother–daughter associations remained significant after young females were removed from the data set. This allowed us to assess whether adult females associated strongly with their mothers and to verify whether the factors affecting associations between females of all ages were the same as those determining associations between adults only. The random effect multivariate regression tree is a nonparametric dichotomous approach to separate data according to the variable best explaining their distribution. For each new branch, the regression tree renews the calculation and separates data on the basis of the new variable best explaining the separation (Sela & Simonoff, 2009). Dyads were observed over several years, thus we included both members of a dyad as random effects as well as year (2005–2008). For each dyad, relatedness, age and body mass of each female, age and body mass differences, and similarity/difference in reproductive status were included as fixed effects in the model. Relatedness is the 'minimal', true genetic relatedness as calculated by Mainguy et al. (2009) (i.e.

relatedness coefficient for a mother and her daughter = 0.5, for sisters = 0.25, etc.). For body mass, we only included females ≥ 3 years old in the analyses. Mass was adjusted to July 15th according to the average growth rate over the summer of five age groups (3, 4, 5, 6 and >7 years) and taking into account female reproductive status (Festa-Bianchet & Côté, 2008). Similarity in reproductive status was a categorical variable with five categories ('kid' = both females produced a kid that survived that particular summer; 'kid dead' = both females produced a kid, but both kids died during that particular summer; 'no kid' = neither of the females produced a kid; 'mixed' = one female produced a kid (regardless of whether the kid survived or not) and the other did not; and 'mixed kid' = the two females produced a kid, one that survived, the other not). We created a category for females whose kid died because each year about 90% of kid deaths occurred at the same period (within 2 weeks in late May–early June). The size of the trees (i.e. number of nodes) was chosen according to the minimum cross-validation relative error (De'ath & Fabricius, 2000). We verified the significance of the correlation between the HWIG and each variable detected by the regression tree analysis with post hoc Mantel tests (Mantel, 1967) because they take into account the nonindependence of relationships within a group or population (Schnell, Watt, & Douglas, 1985). For each year we tested correlations between HWIGs and variables identified by regression trees. We used the false discovery rate method to control for multiple tests (Benjamini & Hochberg, 1995). Calculations of the significance of the networks, HWIs, HWIGs, Monte Carlo permutation tests and Mantel tests were carried out using Socprog version 2.4 in Matlab v.7.01 (The Mathworks, Natick, MA, U.S.A.). Random effect regression tree analyses were carried out using the procedure RE/EM in R v.2.10 (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Each year, the standard deviation of the observed association matrix was higher than expected if the females associated at random: the probability that the standard deviation of the observed matrix was higher than the random one was always higher than 0.99 over the 4 years of the study. Thus, there were more associations than what could be expected by chance alone; hence the networks were not random. All nodes of the regression tree were significant (Mantel tests, all $P_s < 0.05$) when all females were included in the model, and the mean HWIG of each category selected by the regression tree was higher than 1 (Fig. 1) Relatedness explained the largest proportion of variation in HWIGs (Fig. 1). Highly related females such as mothers and daughters had the strongest associations and thus relatedness appeared at the first node of the tree. This association was especially strong for mothers younger than 9 years of age (mean HWIG = 1.65; Fig. 1). Mothers older than 9 years of age associated less with their daughters than did younger mothers (mean HWIG = 1.21; Fig. 1, Table 1). Daughters' age did not affect the strength of mother–daughter associations because this variable was not selected by the regression tree (Fig. 1).

For less related females, the strongest associations were found for those whose kids survived and for those whose kids died (mean HWIG = 1.09; Fig. 1). In contrast, reproductive status did not influence associations between females of other reproductive status categories (i.e. no kid, mixed, and mixed kid; mean HWIG = 1.01; Fig. 1). In particular, associations between two females that produced a kid but experienced different kid survival associated less often than two females who produced a kid and experienced the same kid survival (i.e. both kids survived or both kids died) (Fig. 1). Body mass did not influence the strength of associations (or it was less important than other factors) because it was not selected by

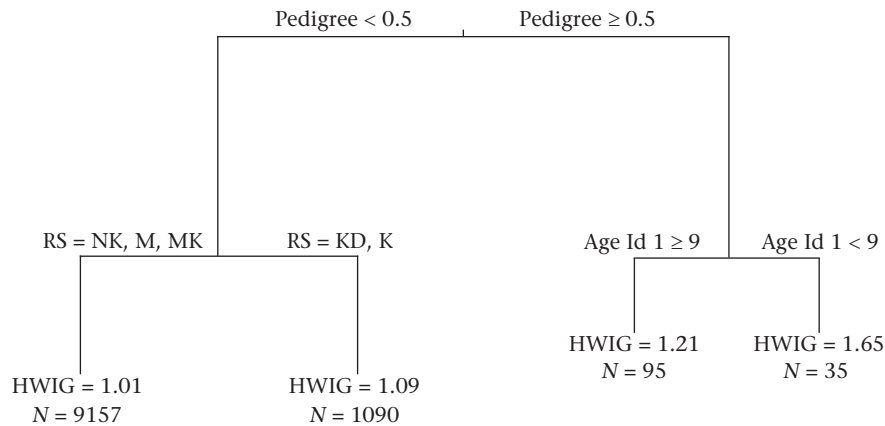


Figure 1. Factors influencing the social structure of female mountain goats from Caw Ridge (Alberta, Canada) for 2005–2008 as shown by a regression tree. Values at the extremity of each branch stand for mean half-weight index corrected for gregariousness (HWIG) for the subgroup determined by the tree, and N provides the number of dyads in that category. Pedigree: 'minimal' true genetic relatedness; RS: reproductive status; NK: neither female of a dyad reproduced; M: one female of the dyad reproduced while the other did not; MK: both females of the dyad reproduced but one of the kids died; KD: both individuals of a dyad reproduced and lost their kids; K: both individuals of a dyad reproduced and their kid survived; Age Id 1: age of the oldest female of the dyad.

Table 1
Mean association strength between female mountain goat mothers and daughters from Caw Ridge (AB, Canada) as calculated with the half-weight index corrected for gregariousness (HWIG) for 2005–2008

	Mothers ≥9 years old			Mothers <9 years old		
	Yearling daughters	2- and 3-year-old daughters	Adult daughters	Yearling daughters	2- and 3-year-old daughters	Adult daughters
m	1.29 (0.41)	1.18 (0.32)	1.22 (0.61)	1.87 (0.70)	1.48 (0.69)	1.30 (0.30)
N	11	32	52	16	17	2

m : averaged HWIG (standard deviation); N : number of dyads.

the regression tree. In addition, females did not associate according to age.

In the next analysis, only adult females (>3 years old) were included. Mantel tests were all significant except for the second node in the left of the regression tree (Fig. 2), for 2005 and 2007 ($P = 0.06$ for 2005 and $P = 0.1$ for 2007 versus $P < 0.001$ for 2006 and $P = 0.001$ for 2008). As for the previous analysis, similarity of reproductive status and relatedness explained most of the variation in HWIGs, but the order in which they appeared in the model was reversed. Females with kids first associated based on the similarity of their reproductive status (mean HWIG = 1.09; Fig. 2, right part of

the regression tree). Females with dissimilar reproductive status and females that did not reproduce associated with each other independently of their reproductive status (mean HWIG = 1.01; Fig. 2, left part of the regression tree). Among these females, mothers and daughters showed stronger associations than unrelated females (mean HWIG = 1.20; Fig. 2), but this association was only significant for 2006 and 2008 ($P < 0.001$ for 2006 and $P = 0.001$ for 2008 versus $P = 0.06$ for 2005 and $P = 0.1$ for 2007). Thus, at least for some years, mothers and adult daughters associated more than unrelated individuals. Body mass and age did not influence the strength of associations.

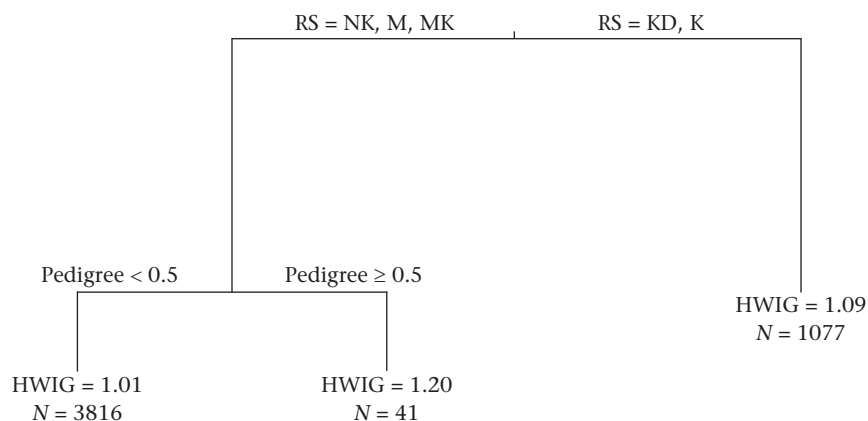


Figure 2. Factors influencing the social structure of female mountain goats >3 years of age from Caw Ridge (AB, Canada) (for 2005–2008) as shown by a regression tree. Values at the extremity of each branch stand for the mean half-weight index corrected for gregariousness (HWIG) for the subgroup determined by the tree, and N provides the number of dyads in that category. Abbreviations as in Fig. 1.

DISCUSSION

We show here that the social network of female mountain goats is not random. Among all variables tested, genetic relatedness and similarity of reproductive status best explained female associations, but their importance varied for sexually immature and adult females. Indeed, when all females were included in the analysis, mother–daughter associations showed the highest HWIG (Fig. 1). When only adult females were included in the model, similarity of reproductive status became the most important variable explaining female association differences (Fig. 2). Excluding younger females decreased dyad numbers by half and thus associations of immature females had a large influence on the network. These females were also less constrained by their reproductive status because they had not started to reproduce yet.

We predicted that a female would associate strongly with related females. Fitness benefits of being associated are higher for kin than for nonkin individuals (Archie, et al., 2006). Such bonds between relatives, however, only occurred between mothers and daughters, a result that confirms observations that some female mountain goats are seen in associations with their daughters for up to several years (Festa-Bianchet & Côté, 2008). Associations may not be strong enough to occur between sisters or more distant kin (Le Pendu, Briedermann, Gerard, & Maublanc, 1995). Mountain goats are very aggressive, and daughters may benefit from associating with their mothers to protect themselves from conspecifics (Festa-Bianchet & Côté, 2008). For example, in bison, *Bison bison*, Green, Griswold, and Rothstein (1989) studied mother–daughter associations for daughters up to 3 years of age and showed that when they were in the same group as their mother, females were more often in the centre of the group and were less displaced by other individuals, which could decrease predation risk and increase foraging efficiency. In contrast, no such associations were observed between females older than 1 year and their mothers in bighorn sheep, *Ovis canadensis*, a species known to be less aggressive than mountain goats (Festa-Bianchet, 1991). Our study also provides new insights into mother–mature daughter associations: mountain goat mothers associated with their adult daughters, especially when at least one of them did not reproduce (Fig. 2; significant for 2006 and 2008). This result is interesting because it was only known that mother and daughter mountain goats remained associated during the first 2–3 years of life and not for longer periods (Festa-Bianchet & Côté, 2008).

Maternal age also influenced the strength of associations with daughters, females younger than 9 years old showed stronger associations with their daughters than older ones. Old mothers had on average older daughters than younger mothers, and the strength of associations may decline with daughters' age, as for Indian Ocean bottlenose dolphins, *Tursiops aduncus* (Smolker, Richards, Connor, & Pepper, 1992) and red deer (Albon et al., 1992). This hypothesis, however, does not hold here, because mothers that were 9 years old or older associated less with their daughters than did younger mothers whatever their daughters' age. The same pattern of association was found in a red deer population: bonds between old red deer mothers and daughters were weaker than those between young mothers and their daughters, but only at high population density (Albon et al., 1992). The Caw Ridge mountain goat population size has increased since 1989 (from 95 individuals in 1989 to 149 in 2008; Festa-Bianchet & Côté, 2008), so density was high during our study period (2005–2008), as for the red deer population. In bighorn sheep, no bond between mothers and yearlings was observed at low density, but at high density mothers associated strongly with their yearlings, particularly when mothers had lost their lamb (L'Heureux, Lucherini, Festa-Bianchet, & Jorgenson, 1995).

Similarity of reproductive status also greatly influenced the strength of female associations, especially for adult females. We predicted that females of the same reproductive status would have stronger associations than females of different reproductive status. Adult females associated more strongly when both produced a kid that survived or a kid that died early after birth, but not when both were barren. Association preferences between reproductive females could lead to a reduction of predation risk (Hamilton, 1971) for example, the presence of several kids in the same group may create a dilution effect that reduces the probability for a given kid to be preyed upon. Lactating females could also choose particularly safe habitats (Ruckstuhl, 2007), which could lead to segregation between lactating and nonlactating females (Barten et al., 2001). Lactating mountain goats stay approximately 20 m closer to escape terrain on average than nonlactating females in June when kids are vulnerable (Hamel & Côté, 2007), but this distance was not large enough for lactating females to form separate groups. Previous studies on the same population have also shown that lactating females spend more time foraging than nonreproductive females, reducing their time spent lying down (Hamel & Côté, 2008); this difference in activity budget could favour the association of lactating females and segregate lactating and nonreproductive females. On the other hand, lactating females forage in the same areas and have a higher biting rate than nonlactating females (Hamel & Côté, 2009), which could allow females of both reproductive status to remain in the same groups. Thus, lactating female mountain goats and nonreproductive ones did not segregate, even if lactating females seemed to prefer to associate with each other. Moreover, nonreproductive females associated with their mothers or daughters even if the other one had a kid (Fig. 2), indicating that females who reproduced and females who did not reproduce could be in the same groups.

Interestingly, females that reproduced but had different reproductive status (i.e. one of the kids died, or 'mixed kid') associated less often than females that reproduced and had the same reproductive status (i.e. females whose kids both survived or both died). Moreover, females whose kids died associated more with each other than with nonreproductive females. This suggests that the production of a kid has long-term effects over the summer on the time budget and energy needs of females, which may in turn affect association patterns. Simply classifying females as lactating or nonlactating may thus be misleading.

In many species individuals associate according to phenotypic characteristics. For example, many fish species form shoals of individuals with similar body length, and for most of them grouping with individuals of similar body length could be a response against predators (Krause, Butlin, Peuhkuri, & Pritchard, 2000). In ungulates, individuals with similar body mass may be more synchronized, which may thus enhance their foraging efficiency (Ruckstuhl, 1998, 1999). Because adult mountain goat females varied in body mass (mean \pm SE = 70 \pm 8 kg), we predicted that differences in body mass would lead to associations between females of similar body mass. This was not the case. It is possible that variation in mass was insufficient to affect associations. For example, Ruckstuhl and Neuhaus (2002) showed that there was a threshold that male–female body mass differences should exceed for sexes to segregate. Alternatively, female differences in body mass may be heritable as in many other ungulate species (Pelletier, Réale, Garant, Coltman, & Festa-Bianchet, 2007; Wilson & Réale, 2006), and associations between mothers and daughters may hide potential association patterns of females with different body masses.

We predicted that age similarity would favour associations, as found in wild female giraffes, *Giraffa camelopardalis thornicroftii* (Bercovitch & Berry, 2013). Lactating bottlenose dolphins associate

and their calves are thus raised together. This creates familiarity between calves, which leads to association by age in this population (Wells, Scott, & Irvine, 1987). In polygynous species, a few males generally sire most of the offspring born in a particular year (McElligott et al., 2001), so that paternal sisters of the same age are frequent. These same-age females may associate because of their relatedness or because of familiarity if they were raised together. Female rhesus macaques, *Macaca mulatta*, associate according to paternal sisterhood and age proximity (Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001). Mountain goats are polygynous (Mainguy et al., 2009; Mainguy, Côté, Festa-Bianchet, & Coltman, 2009) and associate when they are lactating. They could thus show similar associations according to age. However, this was not the case. Because females associated strongly with their mothers, it is possible that females followed their mother's group rather than following familiar or same-age individuals, which could prevent associations by age.

We did not use the HWI index, which is the commonly used index to estimate association strength between individuals. We showed previously that HWIG is more appropriate than HWI because it is less biased than the former in the presence of strong differences in gregariousness between individuals or years, as in our study (Godde et al., 2013). In addition, this is the first time that regression trees, to our knowledge, have been used to describe associations. Our multivariate approach revealed that relatedness and similarity of reproductive status influenced the strength of the associations between female mountain goats. It also allowed us to test for interactions between these factors, for example reproductive status influenced associations only for non-mother–daughter dyads. However, our study was based on group composition data. By doing so, we implicitly assumed that all individuals in a group were associated and interacted together at a uniform rate and in the same manner (Whitehead & Dufault, 1999), which may not be the case because we do not know whether females within a group were distributed randomly or formed subunits determined by the factors studied (Hirsch, 2011). It would be interesting to reconduct the analyses with a network built from associations defined as the nearest neighbour (Risenhoover & Bailey, 1985), for example, or from aggressive interactions. This would provide more precise information about the type of behaviours that shape relations within dyads.

The HWIG index allowed us to carry out long-term monitoring of associations between individuals regardless of individual differences in gregariousness, which is a major improvement for social structure analysis. Using regression trees, we highlighted association patterns over several years in female mountain goats. Our results also provide new insights into the social structure of mountain goats: strong associations were found between females and their adult daughters, and the strength of the associations between females and their daughters decreased with mother's age. More research is needed, however, to determine why the strength of mother–daughter associations decreased in older mothers.

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