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Social relationships among captive female Himalayan tahr

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Abstract

We studied social relationships in a captive group of female Himalayan tahr (*Hemitragus jemlahicus*). Female tahr showed frequent aggression and a strictly linear age-graded dominance hierarchy. Coalitions, in contrast, were rare. Female tahr formed differentiated social relationships, as they interacted with different individuals at widely different rates. A principal component analysis revealed that social relationships were best described along three independent dimensions that we labelled as Affiliation, Agonism and Ambivalence. Both Affiliation and Agonism were directed preferentially down the hierarchy. Affiliation was also directed preferentially to kin, while Agonism showed the reverse pattern. Ambivalence was unrelated to both dominance and kinship. Overall, these results show that an ungulate species can form differentiated social relationships that vary in relation to dominance rank and kinship.

KEYWORDS
affiliation, agonism, dominance hierarchy, *Hemitragus jemlahicus*, kinship, social relationships

1 | INTRODUCTION

In the last twenty years, it has become clear that the social relationships formed by group-living animals have significant fitness consequences. Animals forming stronger social bonds or having a more central position in the social network have been shown to enjoy greater survival and reproduction (e.g., Bond et al., 2021; Cameron et al., 2009; Frère et al., 2010; Silk et al., 2010; Vander Wal et al., 2015; see Snyder-Mackler et al., 2020 for a review).

An unintended effect of this emphasis on the fitness consequences of social life is that it has promoted a somewhat simplified view of social relationships, that are conceived as essentially monodimensional. In this simplified view, the social relationship linking two animals can vary from weak to strong along a single dimension that is then correlated with the fitness measure of interest. Although valuable for investigating the evolution of sociality, this simplified view of social relationships contrasts with the results of studies aimed at analysing the details of the social life of animals. Building on the seminal work of Robert Hinde (1976, 1983), studies conducted mainly in nonhuman primates have revealed a complex social life that includes at least three different characteristics: first, highly differentiated social relationships, meaning that individuals interact in sharply different ways with their different group

mates (Silk et al., 2006); second, multidimensional social relationships, meaning that the variability in social interactions is best described considering variation along more than one dimension (Fraser et al., 2008; Rebecchini et al., 2011); third, the presence of sophisticated mechanisms for managing social relationships, including reconciliation and complex patterns of coalition formation (Aureli et al., 2012; Harcourt & de Waal, 1992).

The extent to which this complex social life is unique to primates or is shared with nonprimate species has been a matter of debate (Harcourt, 1992; Rowell, 1999; Rowell & Rowell, 1993; Schino, 2000; Wrangham, 1983). It is now becoming progressively evident that several characteristics of social life that were thought to be unique to primates are in fact shared by other socially living species, including multidimensional and differentiated social relationships (giraffes, *Giraffa camelopardalis*: Bashaw et al., 2007; ravens, *Corvus corax*: Fraser & Bugnyar, 2010; domestic pigs, *Sus scrofa*: Goumon et al., 2020), complex coalition formation (plains zebras, *Equus quagga*: Schilder, 1990; spotted hyenas, *Crocuta crocuta*: Zabel et al., 1992) and reconciliation (wolves, *Canis lupus*: Cordoni & Palagi, 2008; ravens: Fraser & Bugnyar, 2011; domestic goats, *Capra hircus*: Schino, 1998), although such characteristics are not necessarily present in all social animals (rats, *Rattus norvegicus*: Schweinfurth et al., 2017).

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Even a cursory look at the literature, however, shows that behavioural ecology (in the wild) and cognition (in the lab) are much more common topics of studies of nonprimate species than detailed studies of social relationships and social strategies (Kutsukake, 2009; Stanley & Dunbar, 2013). In this study, we contributed to correct this imbalance by studying social relationships in a captive group of female Himalayan tahr (*Hemitragus jemlahicus*). We focused on females as this sex is relatively understudied in ungulates. We aimed at describing patterns of dominance and coalition formation and at analysing the structure of social relationships and its association with kinship and dominance.

The Himalayan tahr is a mountain ungulate that lives in herds characterized by high degrees of fission/fusion dynamics. Females are philopatric and form herds numbering 15–50 animals, including juveniles. Adult males associate with females during the rut, but live in separate groups during the rest of the year (Green, 1978; Lovari et al., 2009, 2015; Sathyakumar et al., 2015; Schaller, 1973).

2 | METHODS

2.1 | Subjects and housing

Subjects of this study were ten female Himalayan tahr, aged 1–13 years, forming a captive group living in the Rome Zoo (Bioparco). They formed three different matrilines numbering 1, 2 and 7 females. Coefficients of maternal relatedness were derived from genealogical records. Originally, the group included also several males, that were separated from the females about a month before the beginning of the study.

The group lived in a 200 m² outdoor enclosure in an area not accessible to the public. The enclosure included natural vegetation and a few climbing structures. The tahr were fed twice a day. In the morning, they received hay and alfalfa, while in the afternoon they received more hay and commercial ungulate pelleted food (see below for details). Water was available ad libitum.

Six of the females gave birth during the study period. Kids born during the study period were not included in the data collection, and any interaction they initiated or received was ignored.

2.2 | Data collection

Data were collected between March and June 2021 using an ethogram that integrated published ethograms of tahr and of other *Caprinae* species (Schaller, 1973; Schino, 1998; Shank, 1972). Behaviour patterns recorded during observations are described in Table 1. We carried out two different kinds of observations. Standard observations consisted of 15-min focal animal observation sessions based on a combination of the complete record and instantaneous sampling (every 60 s) techniques. Standard observations were conducted between 0830 and 1800 h and were distributed evenly among females, for a total of 400.75 h of observation.

TABLE 1 Behaviour patterns recorded during the study

Behaviour pattern	Definition	Sampling method	Type of observation
Allogrooming	Oral scraping and licking movements directed at the recipient's fur	Complete record	Standard observations
Muzzle-muzzle contact	Any nonagonistic contact between the animals' muzzles	Complete record	Standard observations
Muzzle-body contact	Any nonagonistic contact between the muzzle of the actor and the body of the recipient	Complete record	Standard observations
Gentle horn contact	A gentle contact between the actor's horns and the recipient's body, head or horns	Complete record	Standard observations
Butt	A forward and downwards strike with the head in which the horns come into contact with the recipient body	Complete record	Standard observations
Parried butt	Same as Butt, but the strike is parried by the recipient's horns	Complete record	Standard observations
Reciprocal butt	Same as Parried butt, but the strike is reciprocal and directed at the adversary's horns	Complete record	Standard observations
Butt threat	A brief and rapid lowering of the head directed at the recipient, that is, a butting intentional movement	Complete record	Standard observations
Chase	Meaning obvious; it includes short (1–2 m) rushes	Complete record	Standard observations
Approach	Actor approaches recipient (distance decreases from >1 to <1 m)	Complete record	Standard observations
Leave	Actor leaves recipient (distance increases from <1 to >1 m)	Complete record	Standard observations
Supplant	Actor approaches recipient, who leaves immediately (within 5 s)	Complete record	Standard observations
Proximity	Subject is within 1 m of another individual	Instantaneous sampling	Standard observations
Co-feeding	Subject is present in the feeding area together with another individual	Instantaneous sampling	Feeding observations

Feeding observations were done in the afternoon, at the time the keepers fed tahr with commercial pellet, a highly preferred food. The keepers distributed pellets in 2–3 areas of a few square meters each. The observer selected one of the feeding areas and recorded every 15 s the identity of all the animals present in the area. The observation ended when no animal was observed feeding for two minutes. A total of 34 feeding observation sessions were completed (average number of sampling points per session: 55.1; range: 9–96).

2.3 | Data analysis

We determined the dominance hierarchy and its linearity using the I&SI method as implemented in DomiCalc (de Silva et al., 2017; Schmid & de Vries, 2013). We included into the analysis all unidirectional aggressive interactions (i.e., Butt, Parried butt, Butt threat and Chase). In order to evaluate the factors affecting dominance, we entered individual dominance ranks into a linear regression whose independent variables were the age of the subjects and the number of kin they had in the group. We also entered dyadic unsigned rank differences into a linear mixed model that included the unsigned age difference and the degree of kinship between the two members of the dyad as independent variables and the identities of the two members of the dyad as crossed random effects.

We recorded a coalition whenever a third individual joined within 30 s an aggressive interaction attacking either the initial aggressor (victim support) or the initial recipient (aggressor support). We calculated dyadic scores of support dividing, for each dyad, the number of episodes of support by the number of occasions for support (i.e., the total number of aggressions initiated and received by the recipient of support minus the number of aggressions exchanged between the supporter and the recipient of support). Dyadic support scores were entered as the dependent variable of a linear mixed model that included the signed rank difference and the degree of kinship between the two members of the dyad as independent variables and the identities of the two members of the dyad as crossed random effects.

We calculated dyadic scores for each of the behaviour patterns shown in Table 1. With the exception of allogrooming, dyadic scores for all behaviour patterns recorded using the complete record technique were calculated as hourly rates (e.g., number of butts per hour of observation directed by animal A to animal B). Dyadic scores for allogrooming were calculated as seconds of grooming per hour of observations. Dyadic scores for proximity were calculated as proportions of sampling points in which the two individuals were recorded in proximity. Dyadic scores for co-feeding were calculated as number of sampling points in which animals A and B were simultaneously present in the feeding area divided by the total number of sampling points in which A was present in the feeding area.

We entered dyadic scores for each of the behaviour patterns shown in Table 1 into a principal component analysis (PCA). PCA is a statistical technique that allows to reduce the observed variation to a few independent components based on the pattern of correlation between the variables entered into analysis. Behaviour patterns that had a factor loading higher than 0.6 were used to interpret the components extracted by the PCA. From the PCA, we obtained scores for each dyad and each component. These dyadic component scores were entered as the dependent variables of linear mixed models that included the signed rank difference and the degree of kinship between the two members of the dyad as independent variables and the identities of the two members of the dyad as crossed random effects.

We estimated significances using bootstrap standard errors based on 10,000 permutations. All analyses were run using Stata 17.0 (StataCorp, 2021).

3 | RESULTS

3.1 | Dominance hierarchy and coalition formation

The I&SI method revealed a strictly linear dominance hierarchy (Landau's h' = 0.952, $p < .001$). Dominance rank was predicted by age, with older females attaining higher dominance ranks (coeff. = −0.660, z = −3.17, N = 10, p = .002; Figure 1), but not by the number of kin present in the group (coeff. = 0.069, z = 0.30, N = 10, p = .761). The unsigned rank distance between two females was predicted by their unsigned difference in age (coeff. = 0.566, z = 10.86, N = 90, $p < .001$), but not by their degree of kinship (coeff. = 0.809, z = 0.85, N = 90, p = .397).

Aggression was relatively frequent. Female tahr showed aggression towards their group mates an average of 1.48 ep./h (range 0.30–3.27 ep./h; compare with Figure 1 in Fournier & Festa-Bianchet, 1995). Coalitions, in contrast, were rare. Out of 1126 aggressive episodes recorded, only 29 (2.58%) involved three or more individuals (i.e., represented an aggressive coalition). In 22 out of 29 coalitions (75.86%), a third individual joined the initial aggressor (aggressor support), while in the remaining 7 the third individual attacked the initial aggressor (victim support). Support during
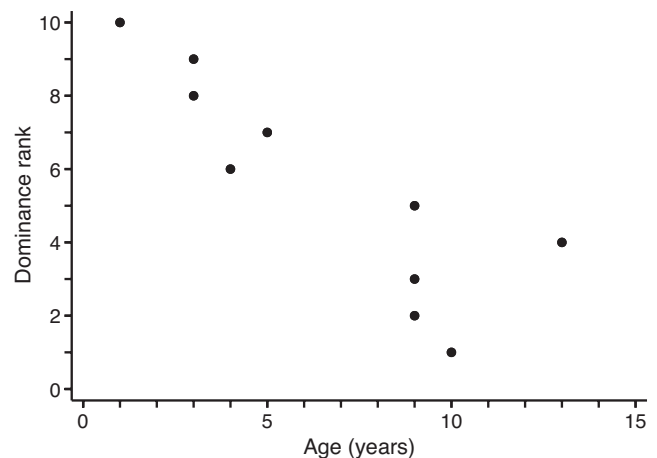

FIGURE 1 Relation between age and dominance rank. Smaller rank values indicate higher dominance ranks

agonistic interactions was not directed preferentially to help kin (coeff. = 0.035, $z = 1.16$, $N = 90$, $p = .244$) or higher-ranking animals (coeff. = −0.001, $z = −1.00$, $N = 90$, $p = .317$).

3.2 | Distribution of affiliation, aggression and cofeeding

All subjects showed at least a few episodes of grooming, other affiliative behaviours, aggressive behaviours and cofeeding. Grooming was the most common affiliative behaviour. Female tahr did not distribute their grooming evenly among group mates. On the contrary, each female showed marked preferences for a few partners and ignored most of the other group mates. Out of 90 possible dyads in our group, grooming was observed in only 26 dyads. The distribution of grooming among the different dyads was therefore highly skewed (skewness = 5.64, $t = 21.85$, $df = 88$, $p < .0001$; Figure 2a). Other affiliative behaviours (that included muzzle-muzzle contact, muzzle-body contact and gentle horn contact) showed a similar distribution among females (skewness = 4.60, $t = 17.83$, $df = 88$, $p < .0001$; Figure 2b). Aggressive behaviours (that included butt, parried butt, reciprocal butt, butt threat and chase) also showed a

markedly uneven distribution, though perhaps a less extreme one (skewness = 1.78, $t = 6.90$, $df = 88$, $p < .0001$; Figure 2c). Finally, co-feeding showed a less (but still significantly) skewed distribution (skewness = 1.20, $t = 4.65$, $df = 88$, $p < .0001$; Figure 2d).

3.3 | Dimensions of social relationships

We ran a PCA on the distribution across dyads of all behaviour patterns listed in Table 1. The PCA extracted three components that together explained more than 70% of the overall variance. Behaviour patterns that loaded high ($r > 0.6$) on the first component included grooming, muzzle-muzzle contact, muzzle-body contact, gentle horn contact, approaching, leaving and being in proximity (Table 2). We labelled this first component "Affiliation." It explained 38.5% of the observed variance. Behaviour patterns that loaded high on the second component included butt, butt threat, chase and supplant (Table 2). We labelled this second component "Agonism." It explained 22.0% of the observed variance. The only behaviour pattern that loaded high on the third component was reciprocal butt (Table 2). We labelled this third component "Ambivalence." It explained 9.7% of the observed variance.
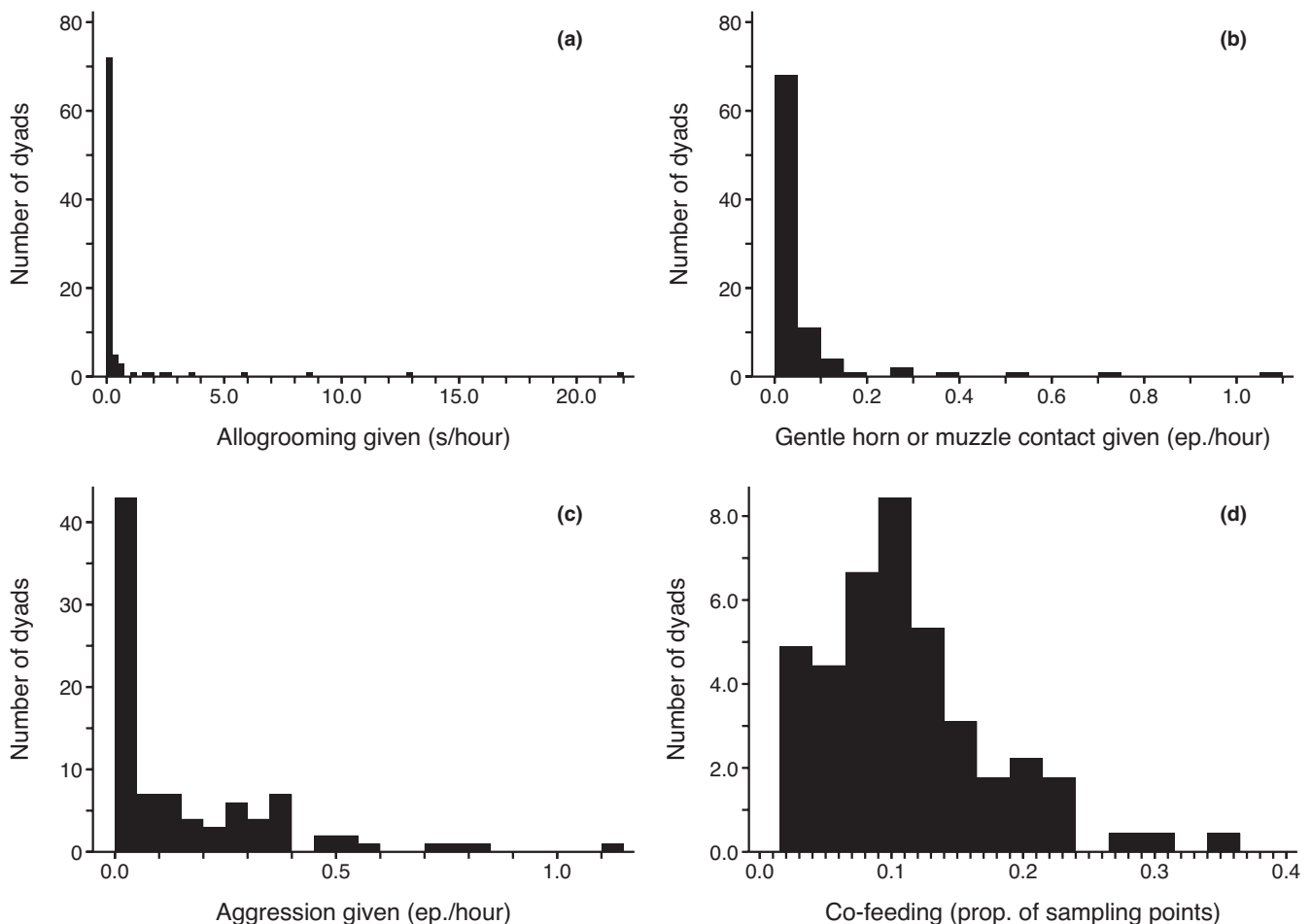

FIGURE 2 Frequency distribution of social interactions. The height of the bars indicates the number of dyads that were observed to interact at the rate shown on the horizontal axis; (a): allogrooming, (b) other affiliative behaviours, (c) aggression; (d) co-feeding

TABLE 2 Loadings (correlation coefficients) of the different behaviour patterns on the three main components extracted by the principal components analysis

Behaviour pattern	Component 1 (affiliation)	Component 2 (agonism)	Component 3 (ambivalence)
Allogrooming	**0.6953**	−0.3211	−0.4138
Muzzle-muzzle contact	**0.8637**	−0.1253	−0.2259
Muzzle-body contact	**0.9061**	−0.1785	−0.0777
Gentle horn contact	**0.7222**	0.2924	0.1949
Butt	0.5862	**0.6554**	0.1806
Parried butt	0.4832	0.2651	0.4925
Reciprocal butt	0.1634	−0.1781	**0.6286**
Butt threat	0.0848	**0.8010**	−0.0877
Chase	−0.2063	**0.7098**	−0.3406
Approach	**0.9095**	0.1941	0.0136
Leave	**0.6594**	−0.4151	−0.3822
Supplant	0.3894	**0.8150**	−0.0683
Proximity	**0.7450**	−0.3931	0.0657
Co-feeding	0.4941	−0.3678	0.3716

Note: Loadings >0.6 are highlighted in bold.

Affiliation was negatively related to rank difference (i.e., it was directed down the hierarchy) (coeff. = −0.130, z = −2.30, N = 90, p = .021) and positively related to the degree of kinship (coeff. = 6.253, z = 3.90, N = 90, p < .001). Agonism was also (unsurprisingly) directed down the hierarchy (coeff. = −0.181, z = −4.19, N = 90, p < .001) and was negatively related to kinship (coeff. = −3.158, z = −2.87, N = 90, p = .004). Ambivalence was unrelated to both rank difference (coeff. = −0.103, z = −1.08, N = 90, p = .280) and kinship (coeff. = 0.913, z = 1.41, N = 90, p = .157). Co-feeding, that was not included in any of the three main components extracted by the PCA, was unrelated to rank difference (coeff. = −0.002, z = −0.97, N = 90, p = .332) and positively related to the degree of kinship (coeff. = 0.265, z = 6.31, N = 90, p < .001).

4 | DISCUSSION

The female tahr of this study formed a strict dominance hierarchy that was largely dependent on age. Age-dependent dominance relationships are common among female ungulates (e.g., mountain goat, *Oreamnos americanus*: Côté, 2000; bighorn sheep, *Ovis canadensis*: Festa-Bianchet, 1991; Alpine chamois, *Rupicapra rupicapra*, Ingold & Marbacher, 1991; Apennine chamois, *Rupicapra pyrenaica ornata*, Locati & Lovari, 1991; red deer, *Cervus elaphus*: Thouless & Guinness, 1986; but see Eccles & Shackleton, 1986, and Fournier & Festa-Bianchet, 1995, for different results) and may be related to the role of body and horn size in determining fighting abilities. Interestingly, among male tahr young adults seem to dominate older individuals (Lovari et al., 2015; see also Locati & Lovari, 1990 for sex differences in the aggressive behaviour of Apennine chamois). The rarity of coalition formation and the absence of a preference for supporting kin may also explain why among female tahr (and possibly among ungulates in general) rank does not seem to be maternally

"inherited," as it happens in several primate species (Walters & Seyfarth, 1986). Understanding why tahr do not aggressively support their kin despite showing a kin bias in affiliation would require a more detailed knowledge of their ecology. It is possible to hypothesize that kin-biased agonistic support is favoured by natural selection only when the distribution of resources makes their collective defence by coalitions of related females profitable and when rank-related differences in reproductive success make the indirect benefits of helping relatives to attain high rank outweigh its direct costs (Schülke & Ostner, 2012). On the other hand, slightly clumped resources may favour both kin-biased affiliation and tolerance (and thus the formation of differentiated social relationships based on maternal relatedness, as observed in this study) and the establishment of clearcut dominance relations (again, as observed in this study; Geist, 1974; see Moscovice et al., 2020, for a more detailed model). Quantifying and comparing the patchiness of resources across different environments and species is a major challenge (Heesen et al., 2014), and not enough information is currently available to test predictions about its effects on social relationships across ungulates (see Geist, 1974, Jarman, 1974; Schaller, 1977 for earlier and somewhat cruder hypotheses and Szemán et al., 2021 for a more recent test).

The female tahr we studied directed most of their affiliative behaviours towards their kin. Although female philopatry is common among female ungulates (making female kin available throughout the lifetime), the extent to which females affiliate preferentially with their kin seems to vary considerably both between and within species (red deer: Albon et al., 1992; Clutton-Brock et al., 1982; bighorn sheep: Festa-Bianchet, 1991; Vander Wal et al., 2016; domestic sheep, *Ovis aries*, Hinch et al., 1990; Lawrence, 1990; Rowell, 1991; impala, *Aepyceros melampus*, Mooring & Hart, 1993; domestic horse, *Equus caballus*, Sigurjónsdóttir et al., 2003). Again, understanding the selective pressures and proximate factors that modulate the preference for kin remains a priority for future studies.

Cords and Aureli (2000) proposed that relationship quality is to be conceived as comprising three different components: relationship Value, Compatibility and Security. The value of a relationship is related to the benefits it engenders to its participants, such as food sharing or allogrooming. The compatibility measures the tolerance between individuals and the general character of their interactions. The security of a relationship relates to the consistency and predictability of their interactions. Investigations based on PCAs of the social relationships of primates and of a single nonprimate species provided empirical support for these theoretical constructs (Fraser et al., 2008; Fraser & Bugnyar, 2011; Majolo et al., 2010; Rebecchini et al., 2011). The results of our study are also coherent with this picture. The first component extracted by the PCA, that we labelled Affiliation, included allogrooming, the most common cooperative behaviour among tahr. It is thus easily interpretable as analogous to the relationship Value of Cords and Aureli (2000). The second component (Aggression) clearly reflects incompatibility and low levels of tolerance, similarly (with an inverted sign) to the Compatibility of Cords and Aureli (2000). Finally, the third component that we observed included reciprocal butt, an indication of an unsettled and possibly inconsistent relationship, similar (again with an inverted sign) to the Security of Cords and Aureli (2000). Overall, the available evidence points to a general consistency in the principles underlying the variation in social relationships among group-living animals, including both primates and nonprimates.

Although little studied in nonprimates, differentiated social relationships seem thus to be common among group-living mammals and birds. Schino and Aureli (2009, 2017) hypothesized that differentiated social relationships are part of the proximate mechanism that allow the reciprocation of cooperative behaviours in the absence of advanced cognitive capabilities (such as the explicit understanding of the costs and benefits involved in the cooperative interaction, or planning abilities). The positive and negative emotional consequences of cooperative and uncooperative interactions were suggested to affect the dynamic of social relationships so that the differentiation of social relationships comes to constitute a system of emotional bookkeeping of the benefits received and costs imposed by group mates (see Massen et al., 2019 for a review of physiological and behavioural correlates). The accumulating evidence that group-living mammals and birds routinely form differentiated social relationships suggests emotionally based reciprocity may be taxonomically widespread, while alternative proximate mechanisms of reciprocity seem to underlie reciprocity in species that do not form differentiated social relationships (Schweinfurth et al., 2017; Schweinfurth & Taborsky, 2020).

Of the three characteristics of complex social life that we identified in the Introduction, two (differentiated and multidimensional social relationships) seem to be present in tahr and to be strongly affected by dominance and kinship. We could not really test the third (the presence of sophisticated mechanisms for the management of relationships). Coalition formation did not seem to play any important role in the social life of tahr, while we did not evaluate

the existence of phenomena such as redirection of aggression or reconciliation.

An obvious limitation of this study is it is being conducted in captivity and on a relatively small and age heterogeneous group. Further research on wild ungulates will be needed to confirm the presence of differentiated and multidimensional social relationships in evolutionarily relevant settings and to assess how ecological variables are related to patterns of social relationships such as the steepness of the dominance hierarchy or the degree of kin bias.

DATA AVAILABILITY STATEMENT

Data will be made available upon reasonable request.

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