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RESEARCH ARTICLE

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Female social dynamics as viewed from grooming networks in the Central Himalayan Langur (*Semnopithecus schistaceus*)

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Abstract
Enhanced survival and reproduction are associated with an individual's direct and indirect social connections with members of a group. Yet, the role of these connections is little known in a vast range of primate species. We studied female Central Himalayan Langur (CHL) to investigate the link between four specific attributes (dominance rank, age, genetic relatedness, and the presence of females carrying infants) and a female's direct and indirect social relationships. By analyzing grooming networks, we revealed different behavioral strategies: high-ranking females form relationships with many females (high degree), whereas females with dependent infants have strong relationships (high strength and eigenvector). Subadult females are important individuals that hold the social network together (high betweenness), while an immigrant female strategy is to integrate herself into the group by forming strong bonds with females who themselves have strong bonds (high eigenvector). Our study sheds light on how behavioral strategies shape female CHL grooming networks, which may help them to secure fitness and survival advantages.

KEYWORDS
colobines, female social bonds, mitochondrial DNA, social network analysis

1 | INTRODUCTION

Animal societies are complex systems in which individuals have nonrandom relationships. These social connections are important elements of an individual's adaptability to cope with their environment (Dunbar, 1988) and are the basic constituent of social structure, that is, the content, quality, and pattern of interaction between individuals (Hinde, 1976); hereafter called social networks. Individual choices for partner associations can impact their reproductive success in many different ways. For example, centrality and dominance rank in the agonistic interaction network of North American bison (*Bison bison*) were positively correlated with the heavier, prime-aged males with the most mating success and offspring sired (Wyman et al., 2021). Central individuals within a social network of three tit species (Family Paridae) were more likely to discover and use novel foraging areas compared to those individuals who have limited social connections (Aplin et al., 2012). Regarding exposure to infectious agents, individuals more centrally located in a group of wild Japanese macaques (*Macaca fuscata*) transmitted simulated pathogens in a shorter amount of time within a grooming network (Romano et al., 2016). In these ways, a network of social contacts can be used to identify possible behavioral strategies that individuals may develop to cope with the costs (competition for resources, disease transmission, resource depletion) and benefits

Abbreviations: AIC, Akaike's information criterion; CHL, Central Himalayan Langur; CR, control region; CYTB, cytochrome b; GLMM, generalized linear mixed-effect models; IT, information-theoretic; mtDNA, mitochondrial DNA; SNA, social network analysis.

(protection from predators, social learning, access to mates) of group living. These strategies include both direct and indirect social connections (Brent, 2015; Firth et al., 2017).

Direct connections (individuals with whom they interact directly) in primates have been linked to individual fitness and processes that can influence individual fitness (e.g., pathogen transmission). For example, free-ranging adult female Chacma baboon (*Papio ursinus*) forming stronger and more stable social bonds with other females experienced greater longevity than females who formed fewer stable relationships (Silk et al., 2010). Female Japanese macaques (*Macaca fuscata*) interacting with more grooming partners had fewer lice than those interacting with fewer partners in winter and summer (Duboscq et al., 2016a). Male Assamese macaques (*Macaca assamensis*) with strong bonds sired more infants (Schülke et al., 2010). While these direct connections provide valuable insight into the benefits of pairwise relationships, it is equally essential to understand the value of an individual's indirect connections (Sih et al., 2009; Sueur et al., 2011; Wey & Blumstein, 2010).

Individuals' indirect connections (partners of their social partners) not only provide a good understanding of their immediate social partners but also the behavioral social patterns of the rest of the group (Wey et al., 2008). An individual's propensity to be indirectly connected may be inherited (Brent, 2015), and is also related to an individual's survival and reproductive success. Such an example comes from male chimpanzees who choose coalition partners who themselves have not formed coalitions with each other yet. This strategy often results in increased connectivity within their social network, which leads to high social rank compared to other males of similar dominance rank and greater reproductive success in terms of offspring sired (Gilby et al., 2013).

Interestingly, individuals may form and adapt social relationships as a behavioral strategy to deal with socioenvironmental pressures. Studies show that individuals get more social connections in the group if they learn about their environment and apply this knowledge to key behaviors such as foraging, predator avoidance, and mate choice (Kulahci & Quinn, 2019). On the other hand, individuals may also "lose" connections (in terms of being socially avoided) if they present signs of infection (Poirotte et al., 2017). Such balance between social attraction and avoidance may be a strategy to manage the costs and benefits of these social interactions (Romano et al., 2020).

A fundamental aspect of primate sociality is the distribution of grooming among group members, which is frequently used as a proxy for the strength of social connections (Dunbar, 1991; Seyfarth, 1977). To quantify this, social network analysis (SNA) has been used to examine variations in grooming behavior in a myriad of species (Torfs et al., 2023). Grooming has been considered to be a low-cost service that individuals can exchange for other kinds of benefits, and this can directly affect how animals distribute their grooming among group members (de Waal, 1997; Schino & Aureli, 2009). The distribution and function of grooming in female primates have been explained by hypotheses that include attributes such as dominance rank, age, genetic relatedness, and the presence of females carrying infants. The hypothesis of "Attraction to high-ranking females" suggests that females compete for the opportunity to groom higher ranking females to receive the benefits provided by them, such as tolerance over food resources and agonistic support during conflicts (Seyfarth, 1976). On the other hand, the "Mothers with infants are attractive social partners" hypothesis proposes that females with infants are the focus of higher levels of social attention as measured by rates of approaches and grooming received, which is linked to the possibility of future opportunities for handling infants. (Gumert, 2007; Seyfarth, 1976; Tiddi et al., 2010). Conversely, the "Attraction to kin" hypothesis, based on social evolution theories, posits that individuals will choose to groom their kin over nonkin due to the advantages of grooming (Chapais & Berman, 2004; Hamilton, 1964; Seyfarth, 1976). In comparable environments, age could potentially influence the formation, maintenance, and function of social connections; however, this aspect has not been extensively studied, particularly among adult female primates (Nakamichi, 2003; Schino & Pinzaglia, 2018).

The genus *Semnopithecus* is comprised of eight species (Roos et al., 2014) and so far, a detailed account of female social relationships has been limited to just two of them. The long-term study sites in Jodhpur and Mount Abu, India, provide the initial detailed description of the Gray Langur (*Semnopithecus entellus*), while the long-term research site in Ramnagar, Nepal, provides details for the CHL (*Semnopithecus schistaceus*) (Borries et al., 1991; Borries, 1993; Koenig & Borries, 2001; Koenig et al., 1998). All three sites are located in the lower elevational range of the *Semnopithecus* genus distribution. Jodhpur and Mount Abu Langurs typically form one-male multifemale groups (Borries, 1993; Hrdy, 1977), while the Ramnagar Langurs have a seasonal multi-male multifemale social organization (Koenig & Borries, 2001). Mount Abu females form a linear dominance hierarchy in which young reproductively active females with infants are higher ranking than others, with old females tending to hold the lowest ranks (Hrdy & Hrdy, 1976). The infants of young high-ranking females are more likely to survive to adulthood than those of lower ranking females. The females of the Jodhpur and Ramnagar populations also exhibit a similar age-based hierarchical structure, in which high-ranking females attain high reproductive success (Borries et al., 1991; Koenig et al., 1998). In general, *S. entellus* and *S. schistaceus* females tend to stay in their natal group, while males disperse at around 6 years of age (Borries, 2000; Hrdy, 1977). In these populations, group composition changes during takeovers, in which a new immigrant male enters the group and replaces the alpha male. Although female dispersal has been reported in *S. entellus* and *S. schistaceus* at these sites, its occurrence is rare, and human disturbance has been described as being a key factor in all documented cases of female dispersal to date (Sterck, 1998).

The primary focus of this study centers on adult females because they tend to allocate a greater portion of their time to grooming compared to individuals in other age-sex categories, particularly within

Old World Monkey groups (Seyfarth, 1976, 1977). The Colobines are known for their broad dietary range and diversity of social systems (Kirkpatrick, 2007). Social grooming is one of the many interindividual social interactions that is widespread in many animal societies (Schino, 2001). While many studies have been conducted on Colobine social grooming, they have primarily focused on examining the amount of time spent grooming within their activity budgets, hence, there is only a limited amount of information regarding the distribution of time spent on grooming with different group members (Matsuda et al., 2015). Currently, there is a lack of information regarding the grooming social network within the Asian colobines (*Semnopithecus* spp.), as well as an absence of understanding regarding the impact of attributes associated with the social grooming hypotheses.

To date, detailed social relationships of this species have been studied only in lower elevation sites. But, interestingly, given the differences in forest composition and climatic conditions at higher altitudes in the Himalayas, CHL living in such environments might exhibit different behavioral strategies. Our study provides a comprehensive investigation of female–female social relationships to address existing research gaps concerning this species in high altitudes. Thus, the aim of this study is to use both direct (degree and strength) and indirect (betweenness and eigenvector) network measures to assess the relative influences of individual attributes, such as dominance rank, age, genetic relatedness, and the presence of females carrying infants, on the variations observed in grooming strategies among wild female Central Himalayan Langurs. Based on the existing social grooming hypotheses (Table 1) and information about primate social networks described above, we make the following predictions: (1) Higher ranking females will have a higher number of grooming partners than lower ranking females. (2) Females with infants will have strong direct and indirect grooming bonds with females. (3) Females with similar haplotypes will develop strong bonds with one another. (4) Young females will present high betweenness centrality (see Table 1 for details).

2 | METHOD

2.1 | Study site and population

The research was conducted in Mandal Valley, Chamoli, Uttarakhand, Garhwal Himalayas, India (30°28′04″N 79°16′31″E, 1500–1800 m above sea level) from May 2017 to November 2018. H. N. established the research site in 2014 when she fully habituated a group (S group) to human observers. S group's home range includes both forests and agricultural fields, frequently putting them close to humans and predatory domestic dogs (Figure 1). All group members, and each newcomer, were individually identified and monitored throughout the study. In 2017, the group contained 71 individuals, including 12 infants, 10 juveniles, eight subadult males, seven subadult females, 28 adult females, and six adult males. In 2018, the group contained 78 individuals, including 10 infants, 11 juveniles, seven subadult males, nine subadult females, 32 adult females, and nine adult males (see Hasegawa et al., 2018; Nautiyal, 2015; Nautiyal et al., 2020; Nautiyal, 2020) for further details of the study site).

2.2 | Behavioral data collection

Data were collected on 34 adult and subadult females for two consecutive mating seasons (see Sugiyama, 1976 about mating season): May–November 2017 and June–November 2018. Our study is focused

TABLE 1 Hypotheses and predictions of the study.

Hypothesis	Predictions	Predictor variables	Based on
High-rank female are attractive social partners Females compete for the opportunity to groom higher ranking females to receive the benefits provided by the highest-ranking females (Seyfarth, 1976).	Higher ranking females will have a higher number of grooming partners than lower ranking females.	Dominance rank (numerical)	Direct connections
Mothers with infants are attractive as social partners Females with infants are the focus of higher levels of social attention as measured by rates of approaches and grooming received, which is linked to the possibility of future opportunities for handling infants (Gumert, 2007; Seyfarth, 1976; Tiddi et al., 2010).	Females with infants will have strong direct and indirect grooming bonds with females.	Presence of female carrying infants (yes/no)	Direct and indirect connections
Attraction to kin Females will choose to groom their kin over nonkin due to the advantages of grooming (Chapais & Berman, 2004; Hamilton, 1964; Seyfarth, 1976).	Females with similar haplotypes will develop strong bonds with one another.	Genetic relatedness (nominal)	Indirect connections
Function of age Young females play a key role in facilitating social connections and interactions between separate or less connected groups of a social network (Nakamichi, 2003; Schino & Pinzaglia, 2018).	Young females will present high betweenness centrality.	Age (nominal)	Indirect connections

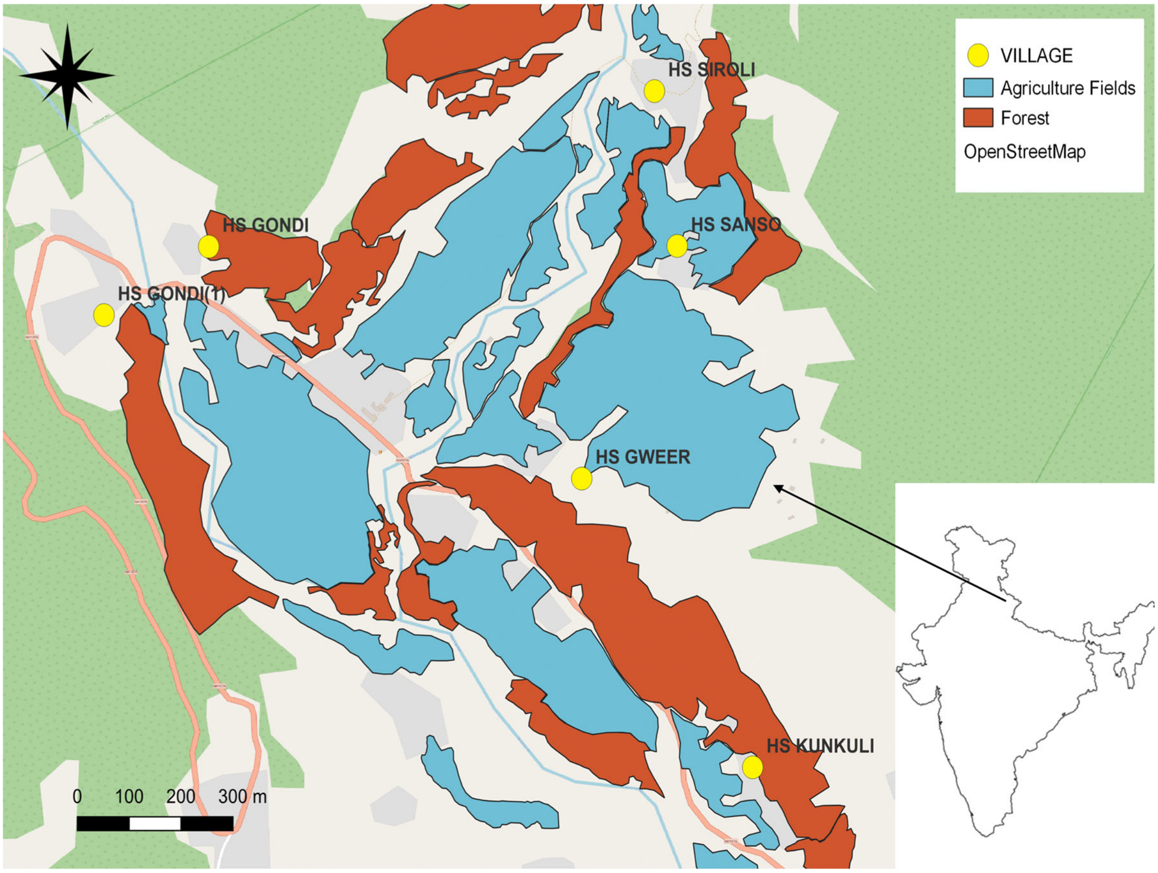

FIGURE 1 Map of study area showing the spatial distribution of forested areas, villages, and agricultural land within the study group's habitat.

on the mating season because during this period, it is generally when all the females have completed giving birth to their offspring. The group was followed from 6:00 a.m. to 6:00 p.m. by two observers (the author, H. N., and a field assistant). Individuals were identified based on morphological features such as body size, shape, fur color, and the presence of scars. To cross-check the identification of individuals between study periods and field assistants, H. N. also created a photographic catalog of every individual. We conducted 15-min focal observations on affiliative behavior, on average 25 days per month, totaling 996 h of observation (493 h in 2017 and 503 h in 2018, Table 2) during the study period. Focal females were selected using a random permutation schedule, with a minimum 30-min interval between observations of the same individual. Female-female grooming interactions were recorded whenever we observed the initiation of a grooming bout. For each bout, we documented the identities of the participants and the duration of grooming for each partner, rounded to the nearest second. Specifically, a grooming bout was defined as a continuous period of grooming involving the same two animals, as outlined by Barrett et al. (1999). Grooming is defined as picking through and/or brushing aside the fur of another, using one or both hands to remove foreign objects on the skin or fur (Dolhinow, 1978). We confirmed interobserver reliability by testing the level of agreement between the two observers (H. N. and H. M.), and found high agreement between them (Cohen's $\kappa = 0.72$). Values between 0.60 and 0.74 are considered good agreement (Watkins & Pacheco, 2000).

2.3 | Noninvasive sample (feces) collection for mitochondrial DNA sequencing

To assess whether each female was born in the group or had immigrated to it, we examined mitochondrial DNA (mtDNA) sequences for all females in the group (Table 2). Fecal samples were collected within a 5-min window after defecation, exclusively when the sample could be linked to the individual's identity. Intestinal epithelial cells were collected from the fecal surface using a cotton swab, which was rubbed across the surface multiple times. The swabs were periodically dipped and stored for future assessment in tubes containing lysis buffer (0.5% sodium dodecyl sulfate, 100 mM ethylenediamine tetraacetic acid [pH 8.0], 100 mM Tris-HCl [pH 8.0], and 10 mM NaCl) (White & Densmore, 1992). Since the amount of DNA obtained from feces was small, each individual was sampled multiple times. Details about the protocol used in these analyses are described in Nautiyal et al. (2023) and Supporting Information S1: Material 1. Following the comparison of 2.4 kb sequences, which encompass the entire sequences of the control region (CR) and cytochrome b (CYTB) gene in mtDNA among adult

TABLE 2 Social characteristics of female Central Himalayan Langurs (*Semnopithecus schistaceus*).

Adult females	ID code	Age	Rank (normalized David score)	Observation hours	mtDNA[a]			mtDNA haplotype
					CR	CYTB	1.8 kb	
Abhi	A	A	18.3	36	LC801044	n.e.	n.e.	Type 1
Abhi2	AB	A	16.74	28	LC801045	n.e.	n.e.	Type 1
Badi	BA	A	15.43	30	LC801046	n.a.	LC801077	Type 1
Beauty	BE	O	18.15	30	LC801047	LC801073	LC801078	Type 1
Geeta	GE	A	16.02	29	LC801048	LC801074	LC801079	Type 1
Goli	GO	A	15.5	34	LC801049	n.a.	LC801080	Type 1
Gulabo	GU	SA	14.28	31	LC801050	n.e.	n.e.	Type 1
Katori[b]	KA	SA	14.89	29				Type 1[b]
Manu	MA	O	20.79	31	LC801051	n.a.	LC801081	Type 1
Meenu	ME	O	17.85	28	LC801052	n.a.	LC801082	Type 1
Naina	N1	A	15.24	28	LC801053	n.e.	n.e.	Type 1
Nalini1	N2	O	17.78	15	LC801054	n.a.	LC801083	Type 1
Nalini2	N3	O	19.2	38	LC801055	n.a.	LC801084	Type 1
Nani1[b]	NA1	O	15.52	26				Type 2[b]
Nani2	NA2	A	16.9	34	LC801056	LC801075	LC801085	Type 2
Neelu	NE	A	16.2	28	LC801057	n.e.	n.e.	Type 1
Peeli	PE	A	16.97	33	LC801058	LC801076	LC801086	Type 3
Pretty[b]	PR	O	17.53	32				Type 1[b]
Rohit	R	SA	14.97	25	LC801059	n.e.	n.e.	Type 1
Sahas	S	A	18.95	36	LC801060	n.a.	LC801087	Type 1
Santa[b]	SA	SA	15.23	26				Type 1[b]
Sanu1	S1	A	15.97	28	LC801061	n.e.	n.e.	Type 2
Sanu2	S2	A	18.01	31	LC801062	n.e.	n.e.	Type 1
Sanu3	S3	A	15.47	27	LC801063	n.e.	n.e.	Type 1
Shakti	SH	A	15.57	39	LC801064	n.e.	n.e.	Type 2
Sheeta[b]	SH1	A	16.86	32				Type 1[b]
Soli	SO	A	16.6	28	LC801065	n.e.	n.e.	Type 1
Sukhveer	SU	A	18.1	31	LC801066	n.e.	n.e.	Type 2
Taklu	TA	SA	15.47	12	LC801067	n.e.	n.e.	Type 2
Tandi	T1	A	14.57	25	LC801068	n.e.	n.e.	Type 1
Tandi jr	T2	SA	17.2	36	LC801069	n.e.	n.e.	Type 1
Tanisha	T3	SA	14.84	28	LC801070	n.e.	n.e.	Type 1
Tashi	T4	SA	14.72	28	LC801071	n.e.	n.e.	Type 1
Teenu	TE	SA	15.01	28	LC801072	n.e.	n.e.	Type 1

Abbreviation of age/sex: A, adult female; mtDNA, mitochondrial DNA; n.a., not amplified in polymerase chain reaction; n.e., not examined; O, old female; SA, subadult female.

[a]MtDNA sequencing was carried out for 29 females using three primer sets which amplify the whole length of the control region (CR) and cytochrome b (CYTB) gene, and the 1.8 kb region which included the whole length of CYTB and hypervariable segment 1 of CR. GenBank Accession numbers of obtained sequences are shown.

[b]MtDNA haplotype assigned based on mother–daughter relationship through behavioral observations.

males and females (Nautiyal et al., 2023), we verified that the CR sequence effectively distinguished the mtDNA haplotypes identified within the study group. Consequently, the classification of mtDNA haplotypes was conducted using the CR sequence, leading to the identification of three distinct haplotypes among the females (as shown in Table 2; GenBank Accession number: LC801044–LC801087).

Regarding the five offspring (KA, NA1, PR, SA, and SH1) in the study group, we could not conduct mtDNA genotyping because fecal samples were not obtained, or the quality of the DNA samples extracted was poor. For this reason, mother's mtDNA genotype was assigned to her offspring. This means that out of the 34 females for which we collected behavioral data, 29 had their DNA sequenced, and for two of them, their mtDNA assignment was based on behavioral observations and birth records: KA, a 4-year-old, is confirmed as the daughter of GE, and SA, a 3-year-old, as the daughter of S. However, for the adult females, NA1-NA2, PR-S2, and SH1-AB, although their mother–daughter relationships were not initially known from birth, we were able to assign haplotypes based on strong social interactions and affiliations among these females (Table 2).

2.4 | Study variables

2.4.1 | Rank

Dominance rank was determined by calculation of David's score (Cheney et al., 2016) based on 763 dyadic interactions. David's scores are valuable as they provide cardinal measures of individual agonistic success that can be subsequently used to examine relationships based on competitive success (de Vries et al., 2006). David's scores are a weighted sum of the individual's dyadic proportions of wins combined with an unweighted and weighted sum of its dyadic proportions of losses. The calculations are based on either the Dyadic Dominance Indices, Dij or Pij, which are in turn computed from the frequencies of dyadic aggressive or submissive behaviors within a group, using an "actor–receiver" matrix format (David, 1987; de Vries et al., 2006). We estimated individuals' social rank by recording the female-female dyadic displacement interactions through ad libitum observations (Altmann, 1974). One individual physically displacing another through peaceful or aggressive means was considered a dyadic displacement interaction (Hrdy & Hrdy, 1976). Due to variations in females' David scores each year, we converted all dyadic displacement interactions into actor–receiver matrices for each year separately. Consequently, the ultimate rank for an individual female is determined by calculating the mean David score over the 2-year period. We used the R package *steepness* for David score analysis (Vries & de Vries, 2014).

2.4.2 | Age

The exact ages of older females were unknown; therefore, females were classified into three age categories based on Borries et al. (1991): young, adult, and old. Young females were those that did not yet have offspring but were sexually mature, while adult females had lactating infants or dependent infants (less than 2 years old). Young and adult females were observed mating during the study. Old females, however, had no dependent infant (less than 2 years old) or juvenile (less than 3 years old) and did not mate in 2017 and 2018. Furthermore, female coat color (which becomes darker with age) and skin wrinkling were also considered in the classification of age (Hrdy, 1977). Among the 34 females, nine were categorized as young, 18 were classified as adults, and seven were in the old age group.

2.4.3 | Genetic relatedness

Female genetic relatedness is categorized based on mitochondrial DNA analysis. Since mtDNA Haplotype 1 was the largest in this group, it is considered that all natal females should have this haplotype. Females of the group's minority mtDNA Haplotypes 2 and 3 are assumed to be relatively recent immigrants.

2.4.4 | Presence of female carrying an infant

In all the models, a binary value of this variable is used to determine whether a female is carrying an infant younger than 1-year-old or not. In 2017, there were seven females with infants younger than 1-year-old, while in 2018, the number of such females increased to 10.

2.5 | Social network analysis and network position

Considering the critical role of grooming in the establishment and maintenance of affiliative relationships in primate societies (Dunbar, 1991; Schino, 2001), we used data from grooming interactions of 34 adult females to build undirected and weighted networks. CHL engage in grooming behavior regularly, typically involving grooming sessions lasting around 1 h, and these sessions occur approximately three to four times daily (Nautiyal, 2015). We estimated individual-level metrics, called "centrality coefficients," to understand the role of attributes on an individual's direct and indirect relationships. We decided to combine the matrices of interaction from 2017 to 2018 to have a broader understanding of the behavioral strategies underlying individual centrality. We used R package *sna* and *igraph* to perform social network analysis, including the estimation of centrality indices (Butts, 2008; Csardi & Nepusz, 2006). In social network analysis, degree, and strength are common direct measures of an individual's centrality, whereas betweenness and eigenvector centrality are common indirect measures (Brent, 2015).

2.5.1 | Degree centrality

It is defined as the total number of connections an individual has in the network (Brent et al., 2011; Wey et al., 2008). In simple terms, it quantifies how well-connected or influential a node is in terms of the number of links it has with other nodes. We calculated degree centrality by counting the total number of grooming partners of an adult female “X” without distinguishing between incoming and outgoing connections. We used the *degree* function from the *igraph* package in R to calculate this. Females with many partners (high degree centrality) are often considered central in their network.

2.5.2 | Strength centrality

It is the sum of the link weights connected to each node (Brent et al., 2011; Wey et al., 2008). Individuals who had many partners and spent a greater amount of time associating with them will have the highest strength centrality (Kurvers et al., 2014; Sueur et al., 2011). We calculated strength centrality by summing the weights, which represent the total time spent, of all grooming interactions an individual female has with each other female. For instance, the calculation for adult female “X” follows this formula: “ScX” = Σ *w*(X, Y) for all females “Y” in the network, *w* meaning the weight of grooming interactions. Strength centrality was calculated in seconds using the *strength* function from the R *igraph* package.

2.5.3 | Betweenness centrality

It is defined as the number of shortest paths that pass through the individual being considered. Individuals with high betweenness tend to interact with individuals who do not interact with one another (Brent, 2015; Freeman, 1977). Therefore, they tend to connect what would otherwise be an unconnected part of the social network. We calculated the number of shortest paths between all pairs of other females in the network that pass through this selected female “X.” Subsequently, we add up the count of these shortest paths that pass through the selected female “X” for every pair of other females in the network. This sum represents the total number of times the selected female “X” acts as an intermediary connecting other females. We used the *betweenness* function from the *igraph* package in R to calculate this.

2.5.4 | Eigenvector centrality

It estimates the connectivity of a node within its network while taking into consideration the connectivity of its neighbors. Individuals with high eigenvector centrality have connections with partners who themselves have a larger number of social partners (Cheney et al., 2016). The Eigenvector centrality (Ec) for female “X” was computed using the following formula: “EcX” = Σ (*w* (X, Y) × Ec(Y)) for all neighbors “Y” of female “X.” In this equation, “w(X, Y)” denotes the weight of the connection between female “X” and “Y,” while “Ec(Y)” represents the eigenvector centrality of each neighboring female “Y” of female “X.” We used the *evcent* function from the *igraph* package in R to calculate this.

2.6 | Statistical analysis

Generalized linear mixed-effect models (GLMM) were built to analyze the impact of social factors on individual network position. We tested the effect of attributes defined above on individual centrality estimated using degree, strength, betweenness, and eigenvector. We developed distinct generalized linear mixed-effect models for each of the four centrality coefficients. Models for degree, strength, and betweenness followed a gaussian distribution, while the eigenvector model followed a gamma distribution. We specified each model with a logit-link function using maximum-likelihood estimation using the function *glmer* from the lme4 package (Bates et al., 2015) in R, version 4.2.2 (R Core Team, 2022). Adult female identity and year were included as a random factor to control for pseudo-replication in all models. We ran tests for homogeneity of residuals and variance inflation factors which suggested no violations of the model assumptions (Field et al., 2012). To evaluate the most parsimonious set of predictor variables that explain the centrality coefficient, we used the *glmulti* package (Calcagno, 2013). Parametric models offer several advantages over permutation methods in nodal and dyadic regression, making them an ideal choice. Specifically, well-specified parametric regression models, such as simple linear regression or mixed models, can be employed instead of node-label permutations (Hart et al., 2022). Moreover, regression models stand out as one of the most commonly used statistical procedures in animal social network analyses (Farine & Whitehead, 2015). They provide a high level of flexibility in model specification and are widely understood and applied in various biological contexts (Dingemanse & Dochtermann, 2013).

Finally, to compare all models simultaneously, we used an information theory approach based on Akaike's information criterion (IT-AIC) (Burnham & Anderson, 2002; Burnham et al., 2011; Richards et al., 2011; Symonds & Moussalli, 2011). The principle of this approach relies on a ranking of the model from the candidate set of models using ΔAICc values ($\Delta i = AIC_{c(i)} - AIC_{c(min)}$) (Burnham & Anderson, 2002). Using the “aictab” function from the package *AICcmodavg*, we measured the model Akaike's weight, or relative likelihood, and accumulative weight of each model that indicates the extent to which model is more likely than another in explaining the variance in the data (Mazerolle, 2016). The likelihood of a particular model being the top choice within a set of models is quantified using standardized model weights (as shown in Supporting Information S1: Materials 2–5). Note that any comparison of multiple models in this framework is relative, not absolute; that is, if a model is identified as the most parsimonious model, this model is considered the best one in the candidate set (Burnham et al., 2011). In recent years, an IT-AIC approach to model-based inference has become increasingly popular across the field of ecology and behavior (e.g., Duboscq et al., 2016b; Garamszegi et al., 2009; Giam & Olden, 2016; Grueber et al., 2011; Johnson & Omland, 2004; Mercier et al., 2017; Whittingham et al., 2006). The model characteristics are presented in Supporting Information S1: Materials 2–5.

3 | RESULTS

3.1 | Network position and attributes

3.1.1 | Direct connections

In the evaluation of degree centrality, the comparison of model weights and AICc differences among the 10 models revealed the strongest support for the "High-rank females are attractive social partners" hypothesis, specifically favoring the model incorporating female dominance rank (weight = 0.61, Supporting Information S1: Material 2). High-ranking females showed greater social connectivity, and had the highest number of grooming partners (high degree), compared to low-ranking females (GLMM; $z = 2.232$, $p \le 0.001$; Table 3 and Figure 2). Regarding *strength* centrality, our results indicated that the model with the presence of a female carrying an infant had the lowest AICc value and the highest model probability (weight = 0.61, Supporting Information S1: Material 3). This lends strong support to the "Mothers with infants are attractive as social partners" hypothesis. Mothers with infants spent a greater amount of time in grooming interactions with other females (high *strength*) than did females without infants (GLMM; $z = 3.982$, $p \le 0.01$; Table 3).

3.1.2 | Indirect connections

From the set of statistical models created, the model combining mtDNA haplotype (genetic relatedness) and age best predicted *betweenness* centrality (weight = 0.43, Supporting Information S1: Material 4). Young females showed more grooming interaction with females who were not grooming each other (high *betweenness*) compared to adult and old females, providing support for the "Function of age" hypothesis (GLMM; $z = 2.320$, $p \le 0.05$; Table 3 and Figure 3). Thus, adult and old females developed grooming interactions with females who are part of their own subgroup (low *betweenness*), while young females form interactions with females who are members of other subgroups (high *betweenness*). Finally, genetic relatedness and the presence of a female carrying an infant emerged as significant predictors of individual eigenvector centrality (weight = 0.38, Supporting Information S1: Material 5). Females with mtDNA Haplotype 2 (considered as immigrant females) engaged in high rates of grooming, particularly with individuals sharing similar haplotypes and those who themselves engage in high rates of grooming (high eigenvector), thus, providing support for the "Attraction to kin" hypothesis (GLMM; $z = -4.579$, $p \le 0.001$; Table 3 and Figure 4). Females carrying infants less than 1-year-old engaged in high rates of grooming with females who themselves engage in higher rates of grooming (high eigenvector) than did females without infants (GLMM; $z = -2.969$, $p \le 0.01$; Table 3).

4 | DISCUSSION

In this study, we investigated the influence of dominance rank, age, genetic relatedness, and the presence of females carrying infants on individual grooming networks to test our four hypotheses regarding the distribution and function of grooming among female CHL using social

TABLE 3 Parameters estimated from generalized linear mixed models (GLMMs) explaining variation in individual centrality of Central Himalayan Langur females.

Centrality coefficients	Predictors	Estimate	SE	*z* Value	*p* Value
Degree	(Intercept)	2.57	5.14	0.256	0.992
	Rank	2.59	0.43	2.232	0.002**
Strength	(Intercept)	445.41	20.61	21.616	<2e−16***
	Presence of female carrying infants	110.33	27.71	3.982	6.84e−05***
Betweenness	(Intercept)	41.93	6.65	6.317	2.66e−10***
	Genetic relatedness (Type 2)	−18.67	18.06	−1.034	0.3011
	Genetic relatedness (Type 3)	−9.59	11.32	−0.87	0.967
	Age (old)	0.43	11.32	0.848	0.398
	Age (young)	27.12	11.69	2.320	0.003*
Eigenvector	(Intercept)	3.514	0.246	14.33	<2e−16***
	Genetic relatedness (Type 2)	−1.405	0.30	−4.579	4.24e−06***
	Genetic relatedness (Type 3)	0.723	0.74	0.974	0.264
	Presence of female carrying infants	−0.690	0.23	−2.969	0.003**

Note: These GLMMs present the lowest AIC within the full list of models available in Supporting Information S1: Materials 2–5.

Abbreviations: AIC, Akaike's information criterion; GLMMs, generalized linear mixed-effect models; SE, standard error.

Statistical significance codes are as follows:

***P < 0.001; **P < 0.01; *P < 0.05.

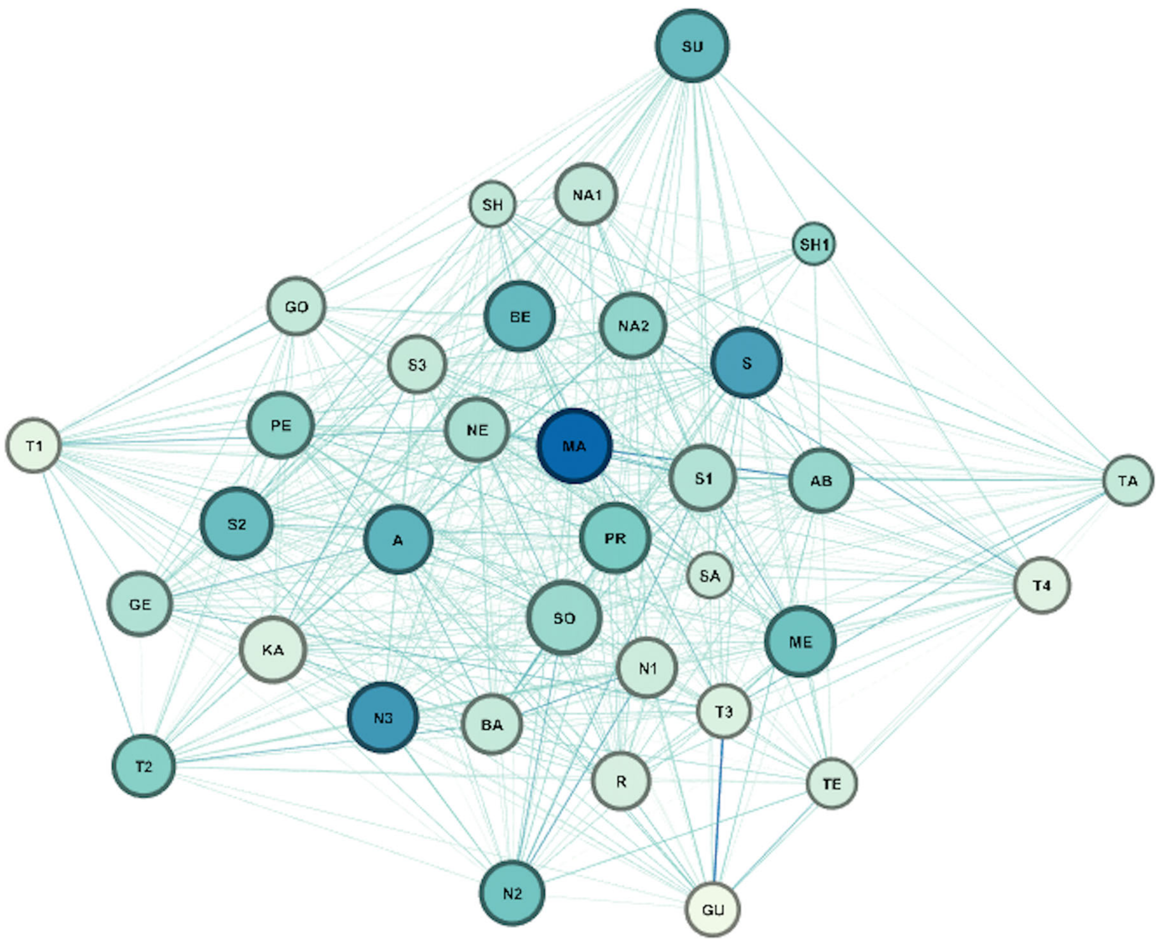

FIGURE 2 Weighted grooming network of Central Himalayan Langur females with a representation of degree centrality (n = 34). Networks were built using Gephi 0.9.2 beta (Cherven, 2013). A node (circle) size represents the individual's degree centrality (the higher the centrality, the larger the node). Nodes are colored according to the rank of the individual (the higher the rank, the stronger is the color of the node).

network analysis. Our data supported these hypotheses. Females with the strongest direct connections were high-ranking females who had a greater number of grooming partners (*degree* centrality, supporting Hypothesis i: high ranking female are attractive social partners). Females with infants had the strongest social bonds (*strength* centrality) and they tended to form strong grooming relationships with other females who also had strong social bonds (*eigenvector* centrality, supporting Hypothesis ii: mothers with infants are attractive as social partners). On the other hand, females with mtDNA Haplotype 2 (considered as immigrant females) like mothers with infants, formed strong grooming relationships with females who themselves had strong bonds (*eigenvector* centrality, supports hypothesis iii: attraction to kin), and subadult females connected more with females who did not interact with one another (*betweenness* centrality, supporting Hypothesis iv: function of age).

4.1 | High-ranking female are attractive social partners

Female CHL exhibited a clear preference for grooming high-ranking females, which resulted in dominant individuals having a great number of grooming partners. This preference for grooming higher ranking females can be explained by the social market theory, which suggests that lower ranking females stand to gain more from interactions with higher ranking individuals (Hammerstein & Noë, 2016; Seyfarth, 1977). The exchange of grooming for agonistic support has been confirmed in several primate species (Schino, 2006), with a growing body of evidence indicating that dominance is associated with fitness benefits (Majolo et al., 2012). In Hanuman Langurs (*Semnopithecus entellus*), for example, high-ranking females have high reproductive success (Borries et al., 1991; Borries, 1993) and strong grooming connections (Borries et al., 1994). However, to our knowledge, in CHL or any *Semnopithecus* species, there is no study specifically investigating the exchange of grooming for agonistic support. Consequently, we recommend that future research focus on investigating these potential benefits within the genus *Semnopithecus*. Such investigations would contribute to a better understanding of the social function of grooming among these primates.

On the other hand, it is worth considering that having a larger number of grooming partners could also provide benefits to

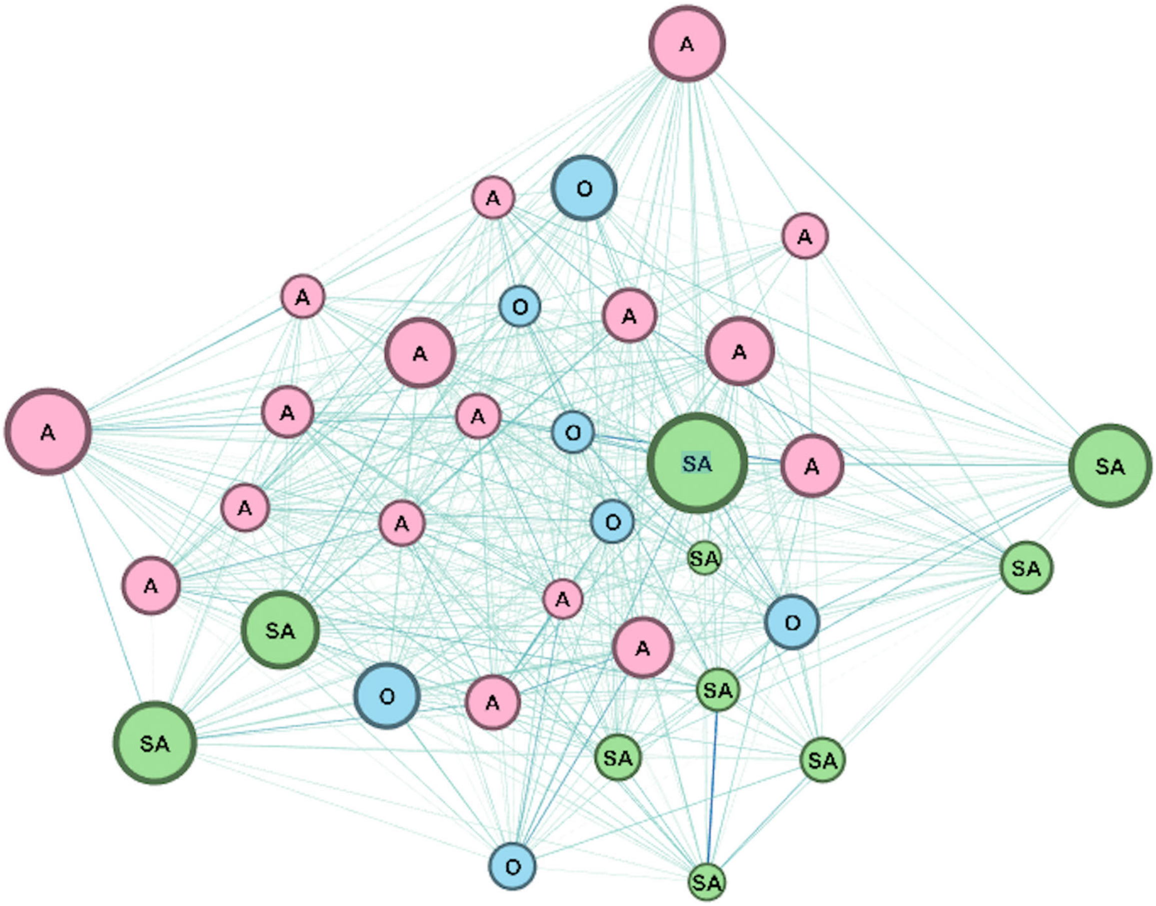

FIGURE 3 Weighted grooming network of Central Himalayan Langur females with a representation of betweenness centrality ($n = 34$). Networks were built using Gephi 0.9.2 beta (Cherven, 2013). A node (circle) size represents the individual's betweenness centrality (the higher the centrality, the larger the node). Nodes are colored according to the age-class of the individual (green nodes—subadult females (SA), pink nodes—adult females (A), and blue nodes—old females (O).

high-ranking CHL females. Under some ecological circumstances, female reproductive success may be affected by the total number of individuals in their network (McFarland et al., 2017). For Barbary macaques (*Macaca sylvanus*), the number of social bonds, but not their strength, predicted survival through a particularly harsh winter (McFarland & Majolo, 2013). Many social animals living in cold environments form groups of individuals to minimize body heat loss (Gilbert et al., 2010). Therefore, primate species inhabiting an extremely cold climate could gain fitness benefits by forming more social bonds (Campbell et al., 2018). High-ranking male Japanese macaques (*Macaca fuscata*) also form a larger huddling group with other kin during cold winter nights (Takahashi, 1997). Huddling close to one another can help Himalayan Langurs stay warm during cold periods since they live in extreme environments, particularly in Himalayan high-altitude locales where temperatures can drop substantially in winter (Nautiyal, 2015; Sayers, 2008). It is likely that high-ranking females strategically invest in forming social connections with a larger number of females, potentially to facilitate the formation of larger huddling groups during the challenging winter months, ultimately contributing to their survival.

4.2 | Mothers with infants are attractive as social partners

Our findings indicate a significant attraction toward females with infants. These females do not only establish strong grooming connections but they also form relationships with females who hold more central positions in the grooming network. According to earlier mammal research applying group-level social network measurements, females spent more time grooming mothers with their infants too (Gero et al., 2013; Wikberg et al., 2015). The inclination to groom females with infants can be explained by the attractiveness of infants, in which females may receive more grooming in exchange for passing their infants to females intensely interested in holding them (Frank & Silk, 2009; Gumert, 2007; Muroyama, 1994; Tiddi et al., 2010). Building a robust social network with allomothers allows mothers to have access to babysitters while foraging, potentially enhancing foraging efficiency (Altmann & Samuels, 1992; Förster & Cords, 2005). It is worth noting that interactions between newborn infants and other group members are common in Hanuman Langurs (Hrdy, 1977), which might lead to increased grooming between mothers and infant handlers. CHL mothers will probably be key

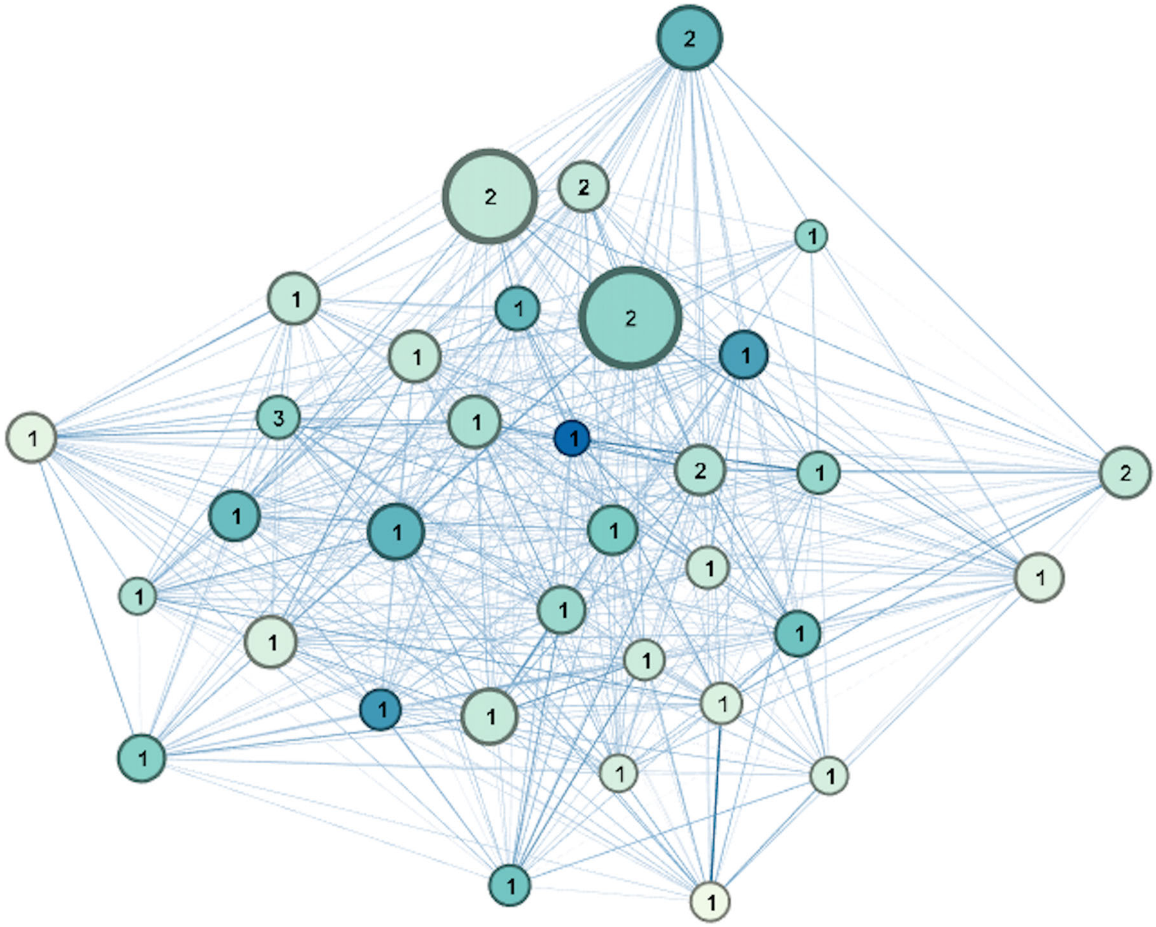

FIGURE 4 Weighted grooming network of Central Himalayan Langur females with a representation of eigenvector centrality (n = 34). Networks were built using Gephi 0.9.2 beta (Cherven, 2013). A node (circle) size represents the individual's eigenvector centrality (higher centrality, larger the node). A node (circle) is colored according to the rank of the individual (the higher the rank, the stronger is the color of the node). Node symbol represent the mtDNA haplotypes; 1—Type 1 haplotype; 2—Type 2 haplotype; 3—Type 3 haplotype.

players in the grooming network because of the interest that allomothers have in mothers and their newborn infants.

However, it is important to emphasize that we did not quantify the direct relationship between grooming and infant handling, leaving room for future studies. Given the high predation pressure at our study site (Nautiyal et al., 2023), forming strong connections with allomothers is likely to benefit infant survival (Silk et al., 2003). Dog predation poses a substantial threat within S group's home range and is the leading cause of infant and juvenile mortality, as documented in our previous study (Nautiyal et al., 2023). Furthermore, the group frequently forages within agricultural areas, which significantly increases their vulnerability to dog attacks (Nautiyal et al., 2020). We reported the injury of three infants due to free-ranging dog predation over 2 years (Nautiyal et al., 2023). In December 2022, we also witnessed a case where, following the death of the biological mother, the orphaned infant was adopted by another female (allomother), and that infant has survived to this day in S group (H. Nautiyal, personal observations). Such infant adoption is a widespread phenomenon and has been documented in over 120 mammalian and 150 avian species (Riedman, 1982). Females who have stronger and more secure social bonds may occupy fewer peripheral positions within the group's spatial distribution (Silk et al., 2009). This may indicate that females with infants receive protection from dog predation, especially when they are engaged in daytime foraging activities within agricultural fields. This finding adds to the body of evidence highlighting the significant influence of females with infants on group-level social network metrics. This impact is particularly relevant in human-dominated habitats with higher risks, as it could be associated with the survival of their infants.

4.3 | Attraction to kin

Knowing the genetic relationships among group members is essential for understanding the evolution of social behavior (Alexander, 1974). In some species, such as yellow-bellied marmots (*Marmota flaviventris*), direct connections are genetically determined, but not indirect connections (Lea et al., 2010). However, in rhesus macaques (*Macaca mulatta*), indirect connections (betweenness and eigenvector) have been shown to display significant heritability (Brent et al., 2013).

In this study, we found CHL females who have mtDNA Haplotype 2 have high indirect connections (high eigenvector centrality) and thus have a larger number of grooming partners who themselves have a larger number of partners. This is interesting because these females have few kin in the group and are considered immigrants. So, indirect connections (such as estimated through eigenvector centrality) may not be heritable in Central Himalayan Langurs. Factors other than kinship may have an impact on patterns of social interaction in populations with female dispersal. As a result, females favor interacting with other females who have similar resource-holding potentials because doing so increases their access to valuable commodities (Colvin, 1983; Henazi & Barrett, 1999; Seyfarth, 1977).

This study indicates a CHL behavioral strategy where immigrant females had strong social bonds with their close kin and also had strong bonds with many natal females who had the most central positions in the network. There is growing evidence of a relationship between eigenvector centrality and fitness. For example, female rhesus macaques with high eigenvector centrality experience high infant survival (Brent et al., 2013), and juvenile male bottlenose dolphins with high eigenvector centrality have a high rate of survival to age 10 (Mann et al., 2012). Female Chacma baboons with high eigenvector centrality have greater offspring longevity (Cheney et al., 2016). Therefore, forming a strong bond with females who also form strong bonds could provide increased fitness benefits to immigrant females in a new group.

4.4 | Function of age

In terms of indirect social connections, primates demonstrate an understanding of third-party relationships (Brent et al., 2014; Cheney, 2011). CHL subadult females occupied network positions with a high level of influence (high betweenness) and groomed females who did not interact with each other. As such, individuals with high betweenness may get fitness benefits with these indirect connections. In male chimpanzees, high betweenness predicted a rise in rank and offspring siring (Gilby et al., 2013). Our data indicate that CHL subadult females have comparatively lower ranks than adult and old females. Subadult females made more indirect connections with other group members, such as grooming females from other subgroups that do not interact with each other, thereby forming a social bridge between otherwise isolated subgroups within the main group. Because subadult females are not high-ranking and do not have infants, they have fewer opportunities to obtain within-group grooming partners or to form strong bonds. Subadult females' indirect connections may facilitate their rise in rank in the future, which in turn can be directly linked to reproductive success.

In conclusion, our results highlight that CHL female attributes associated with the social grooming hypotheses influence their pattern of interaction with others. Our findings provide insights into colobine society, revealing that attributes: dominance rank, age, genetic relatedness, and the presence of females carrying infants, significantly predicted individual centrality within CHL female grooming networks. Extensive habitat loss present significant threats to many primate species worldwide. This study therefore advances our understanding of the social structure of primate species living in the human-dominated landscape. Our research emphasizes the importance of studying various primate social systems and provides insight into the behavioral adaptations of an understudied primate species. This contribution significantly enriches the empirical database essential for constructing and validating models that explore the social and demographic influences on the evolution of primate social relationships.

AUTHOR CONTRIBUTIONS

Himani Nautiyal: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); software (lead); supervision (lead); validation (lead); visualization (lead); writing—original draft (lead); writing—review and editing (lead). **Valéria Romano**: Conceptualization (equal); data curation (supporting); formal analysis (equal); funding acquisition (supporting); investigation (supporting); methodology (equal); project administration (supporting); resources (supporting); software (supporting); supervision (equal); validation (equal); visualization (equal); writing—original draft (supporting); writing—review and editing (equal). **Hiroyuki Tanaka**: Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); software (supporting); supervision (supporting); validation (supporting); visualization (equal); writing—original draft (supporting); writing—review and editing (equal). **Michael A. Huffman**: Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); software (supporting); supervision (lead); validation (supporting); visualization (equal); writing—original draft (supporting); writing—review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supporting Information. The data sets analyzed during the current study are available from the corresponding author on reasonable request.

ETHICS STATEMENT

Our study adhered to Indian wildlife protection laws, complied with the principles for the Ethical Treatment of Nonhuman Primates set forth by the American Society of Primatologists, and followed the Code of Best Practices for Field Primatology as outlined by the American Society of Primatologists. The entire data collection process was noninvasive, and we conducted our research in close collaboration with Indian Forest authorities and the National Biodiversity Board. The research obtained approval from the Field Research Committee Kyoto University's Primate Research Institute.

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