Behavioral ecology of the Central Himalayan Langur (*Semnopithecus schistaceus*) in a human dominated landscape: Multi-species interactions and conservation implications

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ABSTRACT

Habitats dominated by humans and the concomitant fragmentation and conversion of primate habitats are the driving forces behind human-primate conflict interactions, posing one of the greatest threats to primate survival. I investigated the behavioral and ecological adaptability of Central Himalayan Langurs (CHL) (*Semnopithecus schistaceus*) living in a high-altitude small-scale subsistence farming village landscape with fragments of oak patches in the Indian Himalayas. Understanding the social organization of CHL and how this may influence by interactions with humans and predators is important for understanding langurs' adaptation to their environment. I conducted a long-term field study on a fully habituated, individually identified group of langurs to help elucidate four main questions: 1) How do social grooming networks help to maximize individual fitness; 2) What is the source of conflict between CHL and people in a human-modified landscape; 3) What kinds of interactions occur between CHL and their potential predators in an environment not affected by humans 4) What are the behavioral strategies of CHL in response to predation by dogs in the agricultural fields. The grooming network of females was elucidated using social network analysis and mtDNA genotyping to understand the role rank, age, kinship, group membership status (natal, immigrant), mating activity, and the presence/absence of dependent offspring on social organization and their potential impact on individual fitness/survival. High-ranking females had a greater number of grooming partners and females with infants were groomed longer than others. These strong social bonds are known to be beneficial for infant survival. Natal sub-adult and immigrant adult females actively facilitated stronger overall social connectivity of other group members through their broad grooming networks. Immigrant females formed strong grooming relationships with females who themselves had strong bonds, a trait linked in other species to increased fitness. To systematically identify and quantify areas of conflict between humans and CHL, structured interviews of villagers and langur habitat utilization study was conducted. It was revealed that farmers with low agricultural production, possessed more livestock to compensate for livelihood maintenance. These people were most affected by langur crop damage. Villagers with more livestock were also more dependent on oak trees for livestock fodder and firewood, resulting in forest fragmentation and degradation. The villagers perceived this as the major cause for langurs foraging on their agricultural crops. *Quercus leucotricohophora* was found to be critical for langurs as both sleeping and foraging sites in their home range, which overlapped with agricultural fields. In contrast, in a group of CHL studied far from the village, a feeding association between langurs and the Himalayan black bear, a known predator elsewhere, was documented. *Quercus semicarpifolia* was the crucial resource for both species to survive the winter in this habitat. In particular bears with vulnerable young cubs benefited, as they could forage on the ground off the many fruits dislodged by langurs above. In contrast, when langurs in the village group frequently had negative interactions with humans and dogs. In the agricultural fields, langurs were routinely harassed by humans and sometimes fatally attacked and eaten by dogs. In response, longer tenured adult male langurs took a leading role in directly counterattacking predatory dogs and rescuing females and infants stranded in the fields and treeless surrounding areas. This was the first detailed study of the CHL in its high altitude habitat. This study provided behavioral and ecological information valuable for an informed conservation management plan for CHL that also benefits local human inhabitants.

ACKNOWLEDGEMENT

It was back in 2013 when I first went to Mandal valley and observed Central Himalayan langur first the time. I never thought that the group I was observing would lead me on this beautiful journey. They for sure gave me hard times in the field, right from the process of habituating and identifying them. Now this journey reached to the stage that I am writing my PhD thesis on them. There are many people who helped me throughout my journey. Firstly, I am extremely grateful to my advisor Dr. Michael A Huffman. Starting this project from zero was not possible without his support and encouragement. There are countless moments when he helped me to improve my various skills with patience. Thank you so much Mike for giving me immense knowledge. I could not have imagined having a better advisor and mentor for my PhD study.

My completion of the thesis could also not have been accomplished without the guidance of my second advisor Dr. Hiroyuki Tanaka. His expertise in genetics all together gave a different angle to my research. Tanaka-san thank you so much for teaching me complicated genetics lab work with patience. You are also an amazing cook. I learned a lot about Japanese food and culture from you. Thanks for taking an interest in langur DNA work, whenever I have a chance I want to learn more from you.

I cannot express enough thanks to Dr. Anindya Sinha, who helped me to establish my field site in Mandal. I remember the day when I called him from the field and I was frustrated not finding the langurs after several days of searching. He told me one thing, this journey is going to be exiting for you, this is how primatologists establish their field site and come up with exiting new findings. Now after five years I understand what he was talking about that day. If I would have given up that time, it would not be possible to share my exiting findings about these beautiful shy creatures living in the Himalayas.

In the process of obtaining my PhD, I would like to thank my committee members: Dr. Michael A Huffman, Dr. Hiroyuki Tanaka, Dr. Colin Chapman, Dr. James Anderson and Dr. Ikki Matsuda. I am fortunate to have such dedicated committee members. Even with short deadlines, they gave me detailed comments on my thesis despite of their busy schedule, which has been extremely useful for its improvement. My sincere thanks to all of you for your encouragement and believing in me. I am also grateful to Dr. Valeria Romano for her guidance and support. Thanks Valera for teaching me Social Network Analysis from scratch and for getting up early for Skype calls whenever I had doubts. Because of your help I was able to learn so much about langur social life from the angle of their social networks.

I am grateful to each and every one who gave me constructive comments during our weekly Ecology Seminar. Your comments helped me a lot to structure my findings, thank you so much for your efforts in explaining things to me, even after the seminars. I thank the CICASP staff for your patience to help me with complicated paperwork always with smile. I thank CICASP teaching staff for organizing workshops that helped me to build my scientific skills. Working with such an incredible team was a great learning experience for me.

I have no words to Thank Dr. Cecile Sarabian for teaching me numerous things. You were always there for me as friend, family and teacher, thank you so much for everything. I am very grateful to Mr. Josue Alejandro and Nelson Broche for their support. Thanks for taking me grocery shopping and for offering help whenever I needed a Japanese translator. I am also grateful to my little Indian family in Inuyama, Srishti and Sanjana. Particularly during thesis

writing time you both took care of me, as I thought only my mother could do. Thanks for taking care of me and helping me with everything.

I would like to thank my filed assistants Mr. Harish and Mr. Prabhat for working with me till now and helping me in Mandal. I cannot imagine establishing my field site without you guys. I also would like to Thank Mr. Mahesh for helping me with community conservation work and helping with establishing he high-altitude site at 3500 meters. I am grateful to all those villagers who helped me to locate the langurs when I could not find them. For women from small mountain villages in India it would be very hard to do higher education without parents' support. I am fortunate to have supporting parents who believe in me always and also helped me with logistics and support to establish my field site.

All this work would not have been possible without the financial support of many agencies. I thank the Rufford Foundation and National Geographic Society for funding my research at the early stages on my work. I would like to thank Primate Wildlife Science program for constant financial support during my PhD. I am grateful to the Forest Department and The National Biodiversity Board for allowing me to do my research and for permission to transport my samples to Japan for analysis.

CHAPTER 1

GENERAL INTRODUCTION

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Chapter 1

General introduction

In this thesis, my goal was to investigate the behavioral and ecological adaptability of the understudied Central Himalayan langur (CHL) *Semnopithecus schistaeus*, in its high-altitude human-modified environment, and to contribute useful information for their conservation. To do this, I took a multi-disciplinary approach, combining behavioral, sociological, ecological, and genetic information. While a long-term study has previously been conducted on the species at a low-altitude site, Ramnagar in neighboring Nepal, the current study represents some of the first insights based on long-term research of the species in its high-altitude habitat in the central Himalayas. This study expands on the existing body of information about Semnopithecus spp. in the region based on long-term observations of identified individuals and DNA information on kinship. This approach will provide new insights about the species that have not previously been possible to address.

In 2014, I habituated and individually identified S group, in the Mandal valley (1500-2500 masl) and initiated a longitudinal study on it between 2016 and 2018. The group lives in an area surrounding six small subsistence agricultural villages in a remote mountainous region of the Garhwal Himalayas. Shorter-term comparative observations were also conducted on neighboring groups and on another population at higher elevations (ranging around 3000 and above masl) to gain some perspective into differences between langurs in close contact with humans and those that experience relative little interference. One of those studies is included as Chapter 4 this thesis. More of the data from this work remains to be analyzed in the future.

First, the social grooming networks of adult females were investigated to better understand how their distinct patterns of social interactions might help them to survive in this harsh landscape. I also studied the groups' patterns of interaction with predators and humans in their natural and human-modified environments. To better understand the human perspective, I conducted structured interviews on the inhabitants of the six villages located along the valley with varying degrees of interactions with langurs, to understand what they perceived as being the sources of conflict between themselves and langurs. From the langurs' perspective I investigated their use of resources in the habitat and the degree of overlap with those of humans. Another source of conflict in the human dominated habitat are domestic

dogs, left to roam the area around agricultural fields. Dogs pose a significant threat to langurs, which they attack, kill and sometimes consume. To better understand this threat, I studied the behavioral strategies of male CHL for dealing with predation pressure by dogs.

Together, these studies represent the different parts of my thesis work, in the shape of four separate chapters. Before discussing the aims of the thesis and research questions in more detail, some background information is required to inform the reader about the study species, their high altitude habitat the live in and the particular circumstances they face in their habitat.

1.1. Human-modified environments

Habitat change due to anthropogenic activity is a global issue of immense proportions and how mammals respond to these changes in their habitat is a key area of research. One common form of a human-modified landscape is a patch of forest surrounded by agricultural land and settlements. The primates showing the greatest degree of home range overlap with humans are members of genera *Macaca*, *Papio*, and *Cercopithecus* (Hill, 2005). Habitat domination by humans and the concomitant compression, fragmentation, and conversion of primate habitats are the driving forces behind increasing human-primate interaction and one of the greatest threats to primate survival (Laurance et al., 2002; Chapman et al., 2003). To better understand behavioral flexibility and species' adaptive ability, we need to understand how individuals interact with their environment, starting with the effect of such changes in behavior linked to social and demographic contexts (Else, 1991). Although a great number of primate species are currently facing such changes in their habitat, detailed information about behavioral consequences and habitat characteristics are still restricted to a relatively small number of species.

Continued human population expansion has led to deforestation making agricultural and development activities, putting unprecedented pressure on natural habitats around the world. In fact, the UN Population Division estimates that the world's population will rise from 7 billion in 2011 to 9 billion by 2050 (Estrada, 2013). It is not surprising that the increase in human population density corresponds with an increase in the extent of cropland in tropical countries, which globally expanded by 48,000 km2 per year between 1999 and 2008, largely at the expense of forest cover (Phalan et al., 2013). Like the human population, this pattern of land use will also increase, making it necessary to quickly identify what types of species

are most vulnerable to these changes (Onderdonk and Chapman, 2000). In recent decades the loss of primate populations is largely to due to habitat fragmentation, making it critical to understand how fragments are created so that, suitable conservation action can be taken (Marsh, 2013).

Effective conservation action plans can only be made with baseline information on the behavior and ecology of those species under threat. It is important that such studies take place at the early stages of habitat change, identifying and quantifying the function of key tree species for habitat protection and restoration. But knowledge of habitat quality alone cannot provide enough baseline information for conservation action plans. It is equally important to study the behavior and roles of animal species in these changing habitats. Such interactions can provide information about a species' behavioral flexibility, which is important for understanding its overall fitness.

1.2. The Central Himalayan Langur: an enigmatic species

In India, Hanuman langurs (*Semnopithecus* spp.*)* are found in a variety of habitats ranging from the low altitude dry forests of Rajasthan to the high mountain oak forests of the Himalayas (Newton, 1988). Langur taxonomy has undergone several revisions, but currently two recognized species of Himalayan langur can be found in the high-altitude range, Kashmir grey langur (*S. ajax)* and the CHL (Roos et al., 2014). CHL ecologically adapted to higher altitudes of the Himalayas, remain understudied. The taxonomic identity of this species is still uncertain and only recently have efforts begun to resolve its taxonomy on the based on morphology, DNA and ecology (Arekar et al., 2019). The potential vulnerability of this species to climate change has also recently caused alarm, and has led some to suggest that its range is shifting outside of protected areas (Bagaria et al., 2020). One lower altitude population of *S. schistaceus* has been intensely studied for decades at Ramnagar, Nepal (Borries et al., 1999; Perlman et al., 2016; Borries et al., 2017). However, very little is known about the species' behavior and ecology in its typical high-altitude habitat. Preliminary studies of *S. schistaceus* at higher altitudes suggested some distinct behavioral characteristics (Bishop, 1979; Sugiyama, 1976; Curtin, 1982), but despite contributing needed information about the social behavior and ecology of the species, due to the difficulty of locating and following groups in the high-altitude environment, most of these preliminary studies were not

based on individually identified group members. For a deeper understanding of this species' social behavior and ecology, long-term studies based on identified individuals are needed.

In the early 1970s, studies on Hanuman langur (*S. entellus*) focused on male mating strategies and how they related to infanticide. Hrdy (1977) proposed that infanticide is an adaptive behavior, having evolved as a result of intense, post-fertilization, inter-male competition for reproductive access. Infant killing by langur males was explained by the sexual selection hypothesis, which has three main criteria; 1) the male is not related to the infant he kills**,** 2) the death of an unweaned infant shortens the subsequent inter-birth interval of the mother, and 3) the killer increases his chances of mating with the mother and siring her next infant (Hrdy 1974; 1979; Sugiyama, 1984). However, it is noteworthy that neither aggressive group takeover nor infanticide has been observed in Himalayan langur populations (*S. schistaceus*). Early studies by Boggess (1976; 1980; 1982) on (*S. schistaceus*) social behavior and male membership changes described a typical pattern of social organization, with mainly multi-male multi-female groups and a lack of infanticide. These observations were used to challenge the sexual selection hypothesis for infanticide, although why infant killing appears absent in Himalayan langur remains unknown.

Apart from male reproductive strategies, major differences in the behavior and ecology of Himalayan and lowland Hanuman langurs are reported for their social organization, vocalizations, home range use, and feeding ecologies in cold weather (Bishop, 1979; Sayers and Norconk, 2008). Himalayan langur habitats are markedly different from lowland habitats with respect to forest composition and climatic conditions, and these factors play critical roles in the overall ecology of the species. The many studies done on lower-elevation populations have revealed the overall behavior and ecology of the *Semnopithecus* genus, but this information might be of limited value for development of conservation plans of CHL given these primates distinct ecology and behavior, as well as some different kinds of threats.

1.3. Habitat of the Central Himalayan langur: High altitude oak forest

1.3.1. Oak forest: source of livelihood for people

Worldwide, oak forests are found primarily in sub-tropical, temperate, and sub-arctic regions. In the Himalayas different species of oak form an important element of the moist temperate

forest elevation range between 1000- 3500 m above sea level (masl) (Singh et al., 2016). Banj oak (*Quercus leucotrichophora*), an evergreen broadleaf tree, covers extensive areas of the central Himalayas within the 500-2300 masl altitudinal zone (Champion and Seth, 1968; Singh and Singh, 1992; Gairola et al., 2010; Singh et al., 2016). Banj oak is the principal source of fuel to villagers as well as the main fodder tree for their livestock in this zone (Troup, 1921). Banj and other oak species not only provide valuable resources to the local community, but also serve as a major component of the natural habitat, being a key food resource for wildlife (Singh, 1981; Nautiyal and Huffman, 2018; Chapter 3). Oak in the Himalays are well known for their numerous ecosystem services, including protecting soil from erosion and landslide, regulating water flow in watersheds and maintainence of water quality in streams and rivers, and supporting a high native floral and faunal diversity (Singh et al., 2012). These vast oak dominated forests have experienced drastic changes due to anthropogenic activities over the past few decades (Khera et al., 2001; Arya et al., 2011). Excessive dependence of local communities on oak forests for use as grazing lands, removal of branches for fodder and fuelwood, litter removal for cattle bedding and as an agricultural fertilizer, has severely affected regeneration, ultimately causing a major degradation of the region (Rao and Pant, 2001; Rathore et al., 2018). Several studies have concluded that the major factor of Banj oak degredation is excessive dependency and exploitation by local communities (Gupta and Singh, 1962; Thandani and Ashton, 1995).

1.3.2. Oak forest: Key species in the Central Himalayan langur habitat

Quercus species are an important food sources for CHL residing in marginal habitats across the Himalayan range. Sugiyama (1976) reported that *Q. incana* fruits and cambium were the most important food resource for langurs in all six months of his study (post monsoon to winter seasons). For langurs inhabiting the alpine meadows of the Indian Himalayas where food resources are scarce throughout the year and negligible in winter, the main food in their diet before the onset of harsh winter is *Q. semecarpifolia* (Nautiyal and Huffman, 2018; Chapter 3). Research on *S. ajax* by Minhas et al., (2010) suggested that *Q. incana* in the Hindu Kush Himalayas is an essential species used as sleeping trees and as an important food resource in both summer and winter. Similarly, Bishop (1975) notes that in the Nepal Himalayas, *Q. semicarpifolia* are also often used for sleeping trees and is an important food source for *S. schistaceus*. Another study on the same species in the Nepal Himalayas by

Boggess (1980) reported that *Q. semicarpifolia* dominated forest were highly utilized by Himalayan langurs.

While oak is a very important species for maintaining the Himalayan habitat, it also has become a key species for the survival of native fauna. Oaks also have become key resource for local people and has led to drastic changes in the oak forest structure. Oak forests is crucial for the survival of Himalayan langurs, but exactly what role they play is not clearly understood. Although, while all the studies described above on Himalayan langurs have noted the importance of oaks, no studies focusing on the details of how oak are exploited by these primates have been conducted.

1.4. Challenges for primate species in the human dominated landscape

1.4.1. Interaction with people

Human encroachment into forest areas causes habitat fragmentation and brings humans into increasingly contact with other primates and other wildlife, leading to economic loss and an increased potential for zoonotic transmission (McLennan and Huffman, 2012; Nahallage et al., 2008; Huffman and Nahallage, 2013). The loss of habitat and food resources also results in animals encroaching on human settlements, creating socioeconomic issues such as crop foraging by wildlife, and fear of personal harm by local residents, which can lead to retaliatory action against the local wildlife. Although many species forage on cultivated crops, given their high cognitive abilities primates, pose a significant threat, often thwarting attempts to effectively deter them (Naughton-Treves, 1998; Warren et al., 2007)

In addition to alteration to the landscape, people's religious beliefs, hunting, and pet keeping also affect the behaviour and ecology of non-human primates (Fuentes and Hockings, 2010). The human-nonhuman primate interaction is a core component of conservation and an emerging "hot topic" among scientist (Fuentes, 2006). Intensifying human-animal conflicts can complicate efforts to protect and conserve threatened primate species and their habitats. For such efforts to be effective, the attitudes of local communities towards conservation must be understood and their needs and aspirations taken into account (Infield, 1988; Fiallo and Jacobson, 1995).

The effectiveness of wildlife conservation and management programs are affected by a wide array of factors, such as local peoples' perception of the value of wildlife, how they want wildlife to be managed, and how they affect or are affected by wildlife (Decker et al., 2001). An understanding of the ecological and human dimensions of wildlife conflict is important this general context, how crop damage caused by wildlife can affect local peoples' attitudes toward them being especially worthy of more attention (Mir et al., 2015).

1.4.2 Interaction with dogs

When wildlife are in proximity with human it often also encounter human-introduced species. Introduced mammalian predators pose much greater threat to native wildlife compared to any other introduced taxa (Doherty et al., 2017). Furthermore, when introduced species are domesticated animals, such as dogs and cats, they particularly serious conservation challenge due to their close associations with humans, and consequently frequent encounter with wildlife. While the impact of cats on native species has been well documented, the conservation impacts of domestic dogs have only recently received attention (Doherty et al., 2017). The impact of dog on wildlife primarily depends on whether they are free roaming or depend on human provided resources, and proximity to protected areas (Home et al., 2017).

Many primate species are known to interact with dogs (Anderson, 1986), the strategies used to deal with them as serious predators is largely undocumented. CHL interact with dogs (Nautiyal et al., 2020; Chapter 4) when they move to feed in agricultural fields. Langurs living in close proximity to humans may have developed strategies to cope with dogs, but langurs living in protected areas likely to have less detailed knowledge about dogs and thus about their predatory threat. Langurs living in high altitude meadows (far from human settlement) typically do not see dogs, except for during a short period in summer when shepherds bring their livestock to graze the meadows, along with dogs to protect the livestock from predators such as leopard and Himalayan black bear. These dogs have been seen to kill up to 15 CHL in the same day, in an alpine meadow devoid of adequate tree cover for the langurs escape into (Nautiyal, personal communication with sheepherders). Conceivably, CHL sharing habitats with people all year-round have developed strategies to evade dog predation. Understanding such strategies is very important for comprehending the behavioral flexibility of primates in human modified landscapes and seem likely to

influence the primates survival and overall fitness.

Predator avoidance strategies in the forest, habitats far from humans, are similarly important to understand. Leopards are the main predator for the Himalayan langurs, although in Nepal Himalayan black bear also predate on the *S. schistaceus* (Bishop, 1979). While predation is thought to be high in the forest by bear and leopard, due to the dangers and difficulty involved in studying them, studying domestic dogs living in human habitats may provide a unique opportunity to look in detail at the anti-predator behavior of fully habituated and individually identified langurs. In summary: dogs are known to be significant threat to wildlife (Home et al., 2018), but behavioral adaptations to intensive dog predation pressure have never been studied in detail for any wildlife species.

1.4. Aims of the doctoral thesis

The main goals of this thesis are to understand the behavioral and ecological adaptability of the Central Himalayan langur (CHL) in its high altitude human-modified environment, and to contribute baseline information for their conservation. As their interaction with people and predator is key for understanding the adaptation to such an environment, I focused on adaptation by addressing the following questions:

1- What are the behavioral strategies used to maximize fitness in a human modified environment, and do individuals show distinct patterns of social interaction to survive in such landscapes (Chapter 2-5)? I show that in social networks, more centrally positioned individuals will have lower risk of predation (Cheney et at, 2016) and individual with the strongest social ties have greater offspring survival (Silk et al. 2010). Consequently, I predict that immigrant females who have fewer relatives in the group will attempt to make strong connections with natal females to acquire a central position and females with newborn infants will have stronger tie to enhance their infant's survival.

2- What are the important tree species in the CHL habitat and what is the dependency of langur on this species in a human modified environment and undisturbed protected habitats (Chapter 3-4)? Oaks are critical for the conservation of Himalayan forest, therefore, I predict that CHL will depend on oaks for sleeping and feeding.

3- What is there a difference in the pattern of interactions of CHL with people and predators in human modified environments versus protected areas (Chapter 3-5)? I predict that CHL will have negative interactions with people "competition for resources" and dogs "high predation pressure" in human modified environment, although in areas not influenced by humans there may be high levels of neutral or mutualistic patterns of interactions with Himalayan black bear, where predation by them is thought to be low.

4- What are the behavioral strategies adopted by CHL to avoid predation by domestic dogs (Chapter 5). Dogs are frequently interacting with CHL only in the human modified environment, thus I predict that knowledge of dogs will play an important role and that adult males living in the group for longer periods, based on their acquired knowledge, will be the principal protectors of the group.

Finally, I discuss the major adaptation of CHL in such landscapes and what is needed to protect them throughout the Himalayas (Chapter 6). I outline the critical activities urgently needed to bring about coexistence between these langurs and humans and the key element that should be in a Central Himalayan Langur conservation/management plan.

Photo plate: Central Himalayan Langur habitats: **a, b**: natural; **c, d**: human modified

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CHAPTER 2

FEMALE SOCIAL NETWORKS IN CENTRAL HIMALAYAN LANGUR (*Semnopithecus schistaceus)* SOCIETY: CULTIVATING BONDS FOR SURVIVAL IN A PRECARIOUS WORLD

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Chapter 2

Female social networks in Central Himalayan langur (*Semnopithecus schistaceus)* society: cultivating bonds for survival in a precarious world

2.1. Abstract

Enhanced survival and reproduction is associated with individuals who have more or stronger direct and indirect social connections with others in a group. Central Himalayan langurs (CHL) (*Semnopithecus schistaceus*) living in a human modified high-altitude environment were studied to investigate the link between adult female individual traits (rank, age, genetic relationship, fertility, and infant status) and their direct and indirect social relationships with others. Social network analysis was used for the quantification of social structure based on individual level grooming interactions. Rank, and the presence of dependent offspring, age, and mtDNA haplotype predicted the key traits of an individual within social networks. High-ranking females form relationships with many females, whereas females with infants form stronger bonds in their relationships. Sub-adult females are the important age group that holds the social network together, while the immigrant female strategy is to integrate herself into the group by forming strong bonds with those females who themselves have strong bonds with others.

2.2. Introduction

Social structure is defined as dyadic relationships among individuals which reflect behavioral strategies that are selected to maximize inclusive fitness (Kappeler and van Schaik, 2002). Such relationships are an important element of an individual's behavioral flexibility (adaptability) to cope with its environment (Dunbar, 1988). Furthermore, individual choices for partner associations impact their life history, such as the type of information they access, use of resources and reproduction (Farine and Sheldon, 2019). Such patterns of individual choice for partner associations are often represented using social network analysis (SNA) (Kurvers et al., 2014). SNA is a powerful tool for the quantification of social structure (Kurvers et al., 2014; Wey et al., 2008; Sih et al., 2009).

In a social network, the relationship between two individuals includes the content, quality, and

pattern of their interactions, including affiliative, agonistic, cooperative, hierarchical etc. combined, make up a social network, and the basis of a true social system (Hinde, 1976; Barrat et al., 2004; Farine and Whitehead, 2015). Analysis of the social networks of primate societies provides a means of measuring both direct and indirect connections (social relationships) in a group (Brent, 2015). Direct connections (individuals directly interacted with) are the social partners of an individual, and this measure illustrates the strength of connections (nodes) with others, while indirect connections (an indirect association through the interactions of their social partners) demonstrate how individuals are positioned within the wider social network of the group they live in (Silk et al., 2009; Mann et al., 2012; Gilby et al., 2013; Cheney et al., 2016). Identifying the underlying mechanism and functions of social structure of a population is central to many areas of behavioral ecology, evolutionary biology, and conservation (Croft et al., 2011).

Understanding the fitness consequences of direct social connections is a key goal of primate behavioral studies. Therefore, identifying to what degree an individual's strength of social bonds directly linked to the enhancement of its overall fitness and reproductive success is important to fulfilling this goal (Cheney et al., 2016). A long-term study on adult female free-ranging chacma baboons (*Papio ursinus*) showed that those who form stronger and more stable social bonds with other females experienced grater longevity (Silk et al., 2010). Similarly, in adult female yellow baboons (*P. cynocephalus*), those with the strongest ties to other adult females and males lived longer than socially isolated females (Archie et al., 2014). Furthermore, in a group of Drakensberg Mountain baboons (*P. cynocephalus ursinus*), offspring survival was higher for females who formed strong social bonds (Silk et al., 2009), and in a group of Assamese macaques (*Macaca assamensis*), males who had strong bonds with females sired more infants (Croft et al., 2008).

While these direct connections provide valuable insight into benefits of pairwise relationships, it is equally essential to understand the value of an individual's indirect connections (Sih et al., 2009; Wey and Blumstein, 2010; Sueur et al., 2011). Although indirect connections have been linked to an individual's fitness, how such connections work is still not clearly understood (Brent, 2015). Male chimpanzees (*Pan troglodytes*) who interact more with individuals who do not interact with one another (high indirect connections) are expected to increase in rank and also to sire more infants (Gilby et al., 2013). Likewise rhesus macaque (*Macaca mulatta*) males and females who spend a lot of time grooming in proximity to group members who

themselves spend a lot time near others, are more likely to increase their reproductive success (Brent et al., 2013). In short, individual connections beyond dyadic ones can provide a greater understanding of an individual's influence not only on immediate social partners, but also on the rest of the population.

Colobines, also known as leaf eating monkeys, are found throughout Asia and Africa. This group of primates has a broad dietary range and a diversity of social systems (Kirkpatrick, 2007). The specialized colobine digestive physiology allows them to utilize mature leaves during times of food scarcity (Yeager and Kirkpatrick, 1998). This dietary flexibility is one of the reasons they are adapted so well to such a broad range of habitat types, which in turn influences their social system (Hardy, 1977). An understanding of the variability of Asian colobine social systems can be obtained through investigation of the inter-individual relationships among members of identified groups (Matsuda et al., 2012). Thus, detailed information about grooming networks within a group can enhance our understanding of colobine social systems (Matsuda et al., 2015). Central Himalayan langurs (CHL) (*Semnopithecus schistaceus*) an Asian colobine are ecologically adapted to the higher altitudes of the Himalayas. To elucidate the social structure of female CHL this study examined the direct and indirect connections of their relationships within the group's social network. Considering the critical role of grooming in the establishment and maintenance of affiliative relationships in primate societies (Dunbar, 1991; Schino, 2001), female-female grooming networks were analyzed.

Thus far, a detailed account of female Hanuman langur (*Semnopithecus* spp.) social relationships is available from three long-term field sites, the Northern Plains Sacred Langur (*S. entellu*s) of Jodhpur and Mount Abu and CHL in Ramnagar, Nepal. All three sites are located in the lower elevation range of the *Semnopithecus* genus' distribution. Jodhpur and Mount Abu langurs typically form one-male multi-female groups (Hardy, 1977; Borries, 1993), while the Ramnagar langurs have a seasonal multi-male multi-female social organization (Koenig and Borries, 2001). Mount Abu females form a linear dominance hierarchy in which young reproductively active females with infants are higher ranking than others, while old females tend to hold the lowest ranks (Hardy and Hardy, 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, Northern Plains Sacred Langur and CHL females tend to stay in their natal group, while males disperse at around six years of age (Hardy, 1977; Borries, 2000). 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 both of these species, 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).

Due to the loss of important resources in the natural habitat of CHL, several populations inhabiting this zone share proximity with human settlements and frequently forage on agricultural crops, leading to a high frequency of interactions with local people and their predatory dogs (Nautiyal et al., 2020; Chapter 5). A clear understanding of an individual's social interactions will provide a richer understanding of how fitness is achieved and how animals survive in this challenging environment. Thus, the aim of this study is to investigate the link between individual traits (rank, age, genetic relationship, fertility and infant status) and the nature of an individual's direct and indirect relationships, in order to highlight behavioral strategies of female CHL living in a precarious high-altitude environment.

2.3. Method

2.3.1. Study site and population

Research was conducted in Mandal valley, Chamoli, Uttarakhand, Garhwal Himalayas, India (1500 - 1800 meters above sea level) from May 2017 to November 2018. HN established the research site in 2014, and fully habituated a group (S group) to humans. 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, 15 sub-adults, 28 adult females and 6 adult males. In 2018 the group contained 78 individuals, including 10 infants, 11 juveniles, 16 sub-adults, 32 adult females and 9 adult males (see Nautiyal (2015); Hasegawa et al., (2018); Nautiyal et al. (2020) for further details of the study site). Two observers collected behavioral data. Inter-observer reliability was verified before the data was combined for analysis. The level of agreement between the two observers was statistically significant at 0.72 (Cohen's kappa, HN-HM: $k=0.72$, $p<0.001$) (Cohen, 1960). Values between 0.60 and 0.74 are considered good agreement (Watkins and Pacheco, 2000).

2.3.2. Behavioral Data collection

Data were collected on 34 adult females during the period between May 2017-November 2017 and June 2018-November 2018. The group was followed from 06:00 to 18:00. We performed 15 minute focal samples (average 25 days/month; total of 996 hours: 493 hours in 2017 and 503 hours in 2018). One individual physically displacing another is considered as a dyadic displacement interaction (Hardy and Hardy, 1976). Female-female dyadic displacement interactions for rank analysis were collected from *ad-libitum* data (Altmann, 1974).

The study was conducted during the mating season, which starts in early June and ends around late November (Sugiyama, 1976). *Reproductive status* of a female was recorded according to descriptions given by Sommer et al. (1992). We categorized this status from the occurence of the following sexual behaviors: 1- receptive behavior: copulation, sexual solicitatations resulting in a male mounting a female followed by pelvic thrusting, 2- female attractivity: male visual, tactile or olfactory inspection of a female's anogenital area, 3- proceptive behavior: female sexual solicitation towards a male by head-shuddering, lowering of the tail, and presentation of the anogenital area without subsequent copulation.

2.*3.3. Noninvasive sample collection*, *DNA extraction, PCR and DNA sequencing*

To assess whether each adult male and female had been born in the group or if it had immigrated to it, as well as the genetic structure of the group, mitochondrial DNA (mtDNA) sequences were examined for 54 individuals (69 % of all the members of the group and 82% adult and subadults of the group) (Table 1.1 and Appendix Table 1.1). All mother-infant and juvenile relationships are known for the group since 2014, therefore we did not analyze this specific age group thoroughly. In total, 34 females were used to verify the social interactions of females. Among them, 29 females were examined by DNA sequencing. As for the remaining 5 individuals, three were born after 2014 (KA is the 4 year old daughter of GE and SA is the 3 years old daughter of S. For three of the adult females (NA1-NA2 , PR-S2 and SH1-AB) they were assigned as mother-daughter pairs, and haplotypes of the presumed mother, based on their strong social interactions (Appendix Table 2.1). Fecal samples were collected fresh, and only when identity of the individual could be associated with the sample. Using a cotton swab, intestinal epithelial cells were scoured off from the surface of feces by rubbing the swab

multiple times across the surface. The swabs were periodically dipped and twirled in tubes containing lysis buffer [0.5% SDS, 100 mM EDTA (pH 8.0), 100 mM Tris-HCl (pH 8.0), and 10 mM NaCl] (White and Densmore, 1992). Since the amount of DNA obtained from feces was small, each individual was sampled multiple times.

DNA extraction was carried out from the lysate (fecal sample in lysis buffer) using the DNA cleanup system (Wizard SV Gel and PCR Clean-Up System, Promega, Madison, WI, USA), following the method of Kawamoto et al. (2013) with the following minor modification. Before the first step of their procedures, 1 mL lysate was incubated with 40 µL Proteinase K solution (20 mg/ mL) at 65 ˚C overnight. The three mitochondrial regions were examined to detect intraspecific variation in the CHL: the control region (CR, so-called D-loop), cytochrome b gene (CYTB), and the 1.8 kb region that spans the full length of CTYB, tRNA-Thr, tRNA-Pro, and the 1st hypervariable segment (HVS1) of CR. Of the 54, 32 individuals which consisted of 11 adult females, nine adult males and three subadult males were selected for analysis of all the three regions of mtDNA since it was expected that all the haplotypes of the study group would be detected from those individuals, considering langur life history. Then, remaining 22 individuals were examined for CR. Polymerase chain reaction (PCR) was performed to amplify each of the 3 mtDNA regions with a 40 µL reaction mixture [1.5 µL fecal DNA solution, 20.0 µL 2x PCR buffer, 8.0 µL 2mM dNTPs, 1.2 µL forward and reverse primers (10 µM), KOD FX (TOYOBO, Osaka, Japan) and 7.3 µL distilled water]. The thermal cycling condition for all the three regions consisted of the initial denaturation at 94˚C for 2 min, 35 cycles of denaturation at 98 ˚C for 10 sec, annealing at 58 ˚C for 30 sec and extension at 68 ˚C for 1min, and a final extension at 68 ˚C for 5 min. The primers described by Khanal et al. (2018) in PCR of CR and CYTB were used. The primers for PCR of the 1.8 region were designed for this study: forward, 5’-TAATTCAACTACAAAAACAC-3', and reverse, 5’-TTTAAGGGGAACGTGTGGGCG-3’. After PCR, the PCR product was purified using the DNA cleanup system (Wizard SV Gel and PCR Clean-Up System, Promega, Madison, WI, USA). The purified DNA was used in a sequencing reaction with a BigDye Terminator Cycle Sequencing Kit (AppliedBiosystems, Foster City, CA, USA). DNA sequencing was performed with the 3130 Genetic Analyzer (AppliedBiosystems). Sequence data for both directions were confirmed using the Sequence Navigator software (Applied Biosystems).

NUMT (nuclear copies of mitochondria sequences) is one of the problems in PCR and phylogenetic analyses using mtDNA sequence data (cf. Karanth et al., 2008). In the former,

true mtDNA and pseudo mtDNA (from nuclear genome) sequences could be simultaneously amplified, and thus, results of DNA sequencing would not be successful due to overlapping of different DNA sequences. In the latter, results of phylogenetic analysis would produce unusual phylogenetic relationships. In most cases, the NUMT sequence is placed at a deviated position in the phylogenetic tree (Zhang and Hewitt, 1996). One of the reasons for this is that NUMT sequences are evolving slower than true mtDNA sequences. In order to confirm that our sequence data is from true mtDNA, we confirmed that CYTB sequences obtained here could be translated to amino acid, and that frameshifts and/or nonsense mutation did not occur (Collura et al., 1996; Zhang and Hewitt, 1996).

If the CYTB sequence in the 1.8 region is true CYTB gene, the HVS1 region linked to the CYTB is also a true mtDNA sequence. Then, the HVS1 in the 1.8 region was compared to that of CR sequences. Because the HVS1 is a part of CR, if the HVS1 is not a NUMT, a full sequence of CR is also not a NUMT. After this procedure, the sequence data were confirmed as true mtDNA sequences. Translation of CYTB sequences to amino acids was carried out using GENETYX MAC ver. 16.00 (GENETYX, Tokyo Japan).

2.3.4. Individual and social traits

We categorized individuals by age, rank, genetic relatedness, presence/absence of an infant, and reproductive status. The exact age was not known for all females, therefore they were classified in three age categories: 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 two 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 juveniles (less than 3 years old) and did not mate in 2017 and 2018. Furthermore, female coat color (which become darker with age) and skin wrinkling were also considered in the classification of age (Hardy, 1977). Dominance rank was determined by calculation of David's score (Cheney et al., 2016) based on 763 dyadic interactions. All dyadic interactions were converted into actor-receiver matrices for each year separately. The final rank is calculated using the mean David score over two years for each female. I used R package *steepness* for David score analysis (Vries, 2014).

Female genetic relatedness is categorized based on mtDNA 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. Details of these attributes are described in Table 2.1. A proxy for female reproductive status is based only on sexual behavior. I used a binary value in the model (whether the female was mating or not). Similarly, infant status is assigned based on whether a female is carrying an infant, less than 1 year or not.

2.3.5. Social network analysis

We used data from grooming interactions of 34 adult females to build undirected and weighted networks. We then estimated individual level metrics, called "centrality coefficients", to understand the role of individual traits on individual's direct and indirect relationships. We decide to combine the matrices of interaction from 2017 and 2018 as a first step to understand the relationship between individual status and individual centrality. I used R package *sna* (Butts, 2008*)* for analyzing centrality coefficients.

2.3.6. Network position

In social network analysis degree and strength are common direct measures of centrality whereas betweenness and eigenvector are common indirect measures of centrality. Degree centrality is defined as the total number of connections an individual has in the network. Strength is the sum of the link weights connected to each node. Individuals who spend a greater amount of time associating with others will have the highest strength value (Sueur et al., 2011) (Kurvers et al., 2014). Betweenness is the number of shortest paths that pass through the considered individual. Individuals with high betweenness tend to interact with individuals who do not interact with one another (Freeman, 1977; Brent, 2015). Individuals with high betweenness tend to connect what would otherwise be an unconnected part of the social network. Eigenvector is the connectivity of a node within its network, while taking into considering the connectivity of its neighbors. Individuals with high eigenvector centrality have connections with partners who themselves have a larger number of partners (Cheney et al., 2016; Romano et al., 2016).

2.3.7. Genetic relatedness and genetic structure of the group

Classification of mtDNA haplotypes (CR, CYTB and 1.8 kb for each individual) was performed using Sequence Navigator (Applied Biosystems) and GENETYX MAC software. All three data were successfully obtained from most of the adult females and adult males (Table 2.1 and Appendix Figure 2.1). All mtDNA haplotypes detected in the study group were included in the dataset of adult females and adult males.

Genetic structure of S group was reconstructed using the CR data of 54 individuals (Table 2.1). Using GENETYX MAC, the CR sequences were aligned and the NEXUS data file was generated (1086 bp data set). After manually editing the NEXUS data file, cladistic analysis based on Templeton et al.'s (1992) algorithm was performed to estimate genealogical relationships among the individual CR sequences using TCS 1.21 software (Clement et al., 2000; 2002). Frequencies of mtDNA haplotypes were totalled in each age/sex class.

2.3.8. Statistical analysis

Generalized linear mixed-effect models (GLMM) were built to analyze the impact of individual and social factors on individual network position. I tested for significant relationships between centrality coefficients (degree, strength, betweenness, and eigenvector) and the following predictor variables; rank, age, mtDNA haplotype, infant, and mating status. I specified each model with a binomial error structure and logit-link function using maximum-likelihood estimation with the package *lme4* (Bates et al., 2015) in R, version 3.5.3 (R Core Team, 2019). Adult female identity and year was included as random factor to control for pseudo-replication in all models. I ran tests for homogeneity of residuals and variance inflation factors (VIF) which suggested no violations of the model assumptions (Field et al., 2012). To evaluate the most parsimonious set of parameters that can help to explain the centrality coefficient I used the *glmulti* package (Calcagno, 2013). To compare all models simultaneously we used an information theory approach based on Akaike's information criterion (IT-AIC) (Burnham and Anderson, 2002). The principle of this approach relies on ranking of the model from the candidate set of models using ΔAICc values ($\Delta i = AIC_{c(i)} - AIC_{c(min)}$) (Burnham and Anderson, 2002). Using the "aictab" function from the package *AICcmodavg*, I measured the model Akaike's weight, or relative likelihood, and accumulative weight of each model that indicates the extent to which one model is more likely than another in explaining the variance in the data

(Mazerolle, 2016). The model characteristics are presented in Appendix Table 2.2, 2.3, 2.4, 2.5. I used R package *sna* (Butts, 2008) for analyzing centrality measures.

2.4. Results

2.4.1. Social traits of adult females

Of the total 34 females analyzed here, 9 were classified as young, 18 as adult and 7 as old. In 2017, seven females had infants less than one year old, and in 2018, there were 10 such females. Moreover, in 2017, 16 females were actively mating and in 2018, 18 females were doing so. Females with young infants were not observed mating during the study. Three mtDNA haplotypes were found for study group females (Figure 2.1). Of them, 27 have Type 1 haplotype, and are considered to be natal females. The smaller mtDNA haplotype groups Type 2 and 3 consisted of 6 and 1 individuals respectively, and are considered to be immigrant females (see Table 2.1).

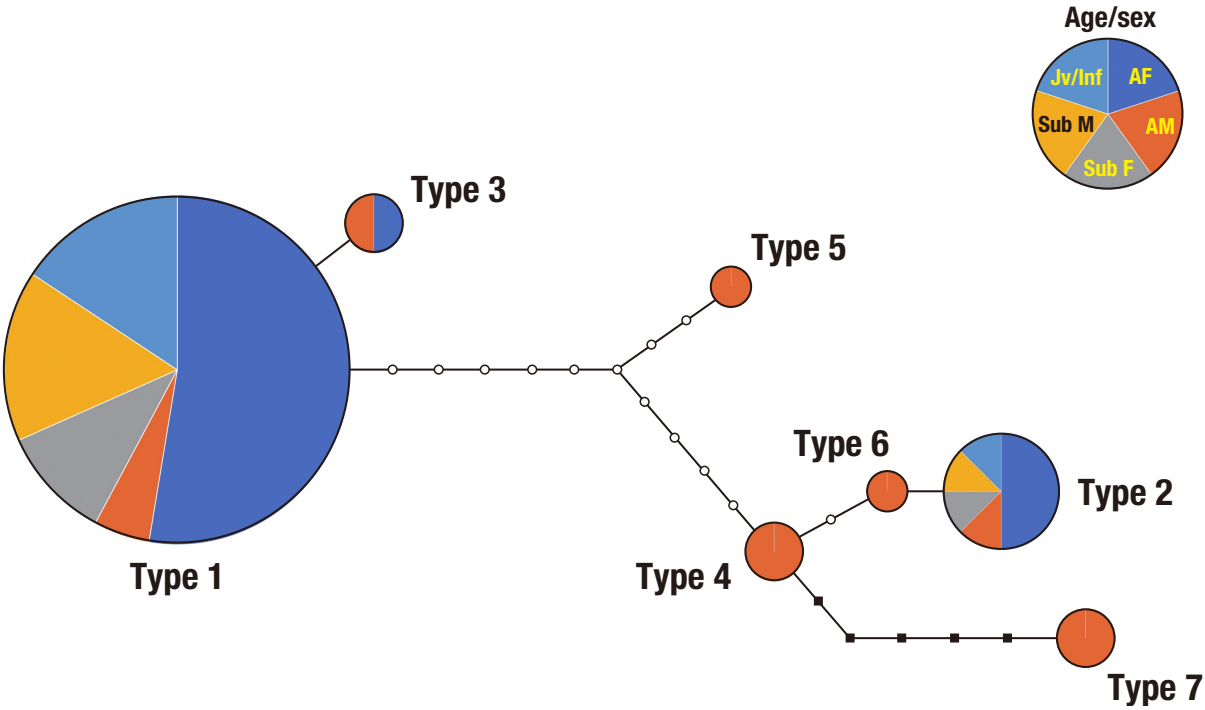


Figure 2.1. Genetic structure of the study group of the Central Himalayan langur (Semnopithecus schistaceus). MtDNA genealogy network was constructed by cladistic analysis based on the algorithm of Templeton et al. (1992) using the control region (1086 bp) data of 54 individuals (see Appendix Table 5.1 and 5.2). A gap was handled as the 5th state. A blank circle and a black square indicate missing haplotypes in the study group. Each step corresponds to a base substitution (○) or insertion/ deletion (■). Abbreviation of age/sex class, AF: adult female, AM: adult male, Sub F: subadult female, Sub M: subadult male, Jv/Inf: Juvenile and Infant of both sexes.

2.4.2 Network position and social traits

Direct connections

I used grooming interactions to investigate the link between network position and social traits. From the set of models created, the model with female dominance rank best explained *degree* centrality (i.e., weight=0.83, Appendix Table 2.2). High-ranking females are the most social because they have the greatest number of grooming partners (high *degree*) compared to low ranking females (z = 3.772, p = <0.001; Table 2.2; Figure 2.2). Results for *strength* centrality indicated that the model combining fertility and infant status have the lowest AICc value and the highest model probability (i.e., weight= 0.17, Appendix Table 2.3). Females carrying infants less than one year old spent a greater amount of time in grooming association with other females, compared to the females without infants, and had (high strength) connections (GLMM; z = 2.702, p = <0.01; Table 2.2; Figure 2.3). However, reproductive status did not

play a role on predicting individual direct relationships (Table 2.2)

Indirect connections

From the set of models created, the model combining mtDNA haplotype (genetic relatedness) and age were the best approximating model for *betweenness* centrality. This model has the lowest AICc value and heights model probability (i.e., weight=0.32, Appendix Table 2.4). Young females have more grooming interaction with females who are not grooming each other (high betweenness) compared to adult and old females (GLMM; z = 2.304, p = <0.05; Table 2.2; Figure 2.4). Thus adult and old females form grooming association with females who are part of their subgroup (low betweenness), while young females form association with females who are members of other subgroups (high betweenness). Results for *eigenvector* centrality indicate that the model combining rank, genetic relatedness and infant status variables have the lowest AIC value high model probability among the set of 12 candidate models (1.e, weight= 0.39, Appendix Table 2.5). Females with mtDNA haplotype 2 (immigrant females) engaged in high rates of grooming with females who themselves engage in high rates of grooming (high eigenvector) (GLMM; z = -4.579, p = <0.001; Table 2.2; Figure 2.5). Although female rank also shows significant effect on eigenvector centrality, though not stronger than mtDNA haplotype (Table 2.2).

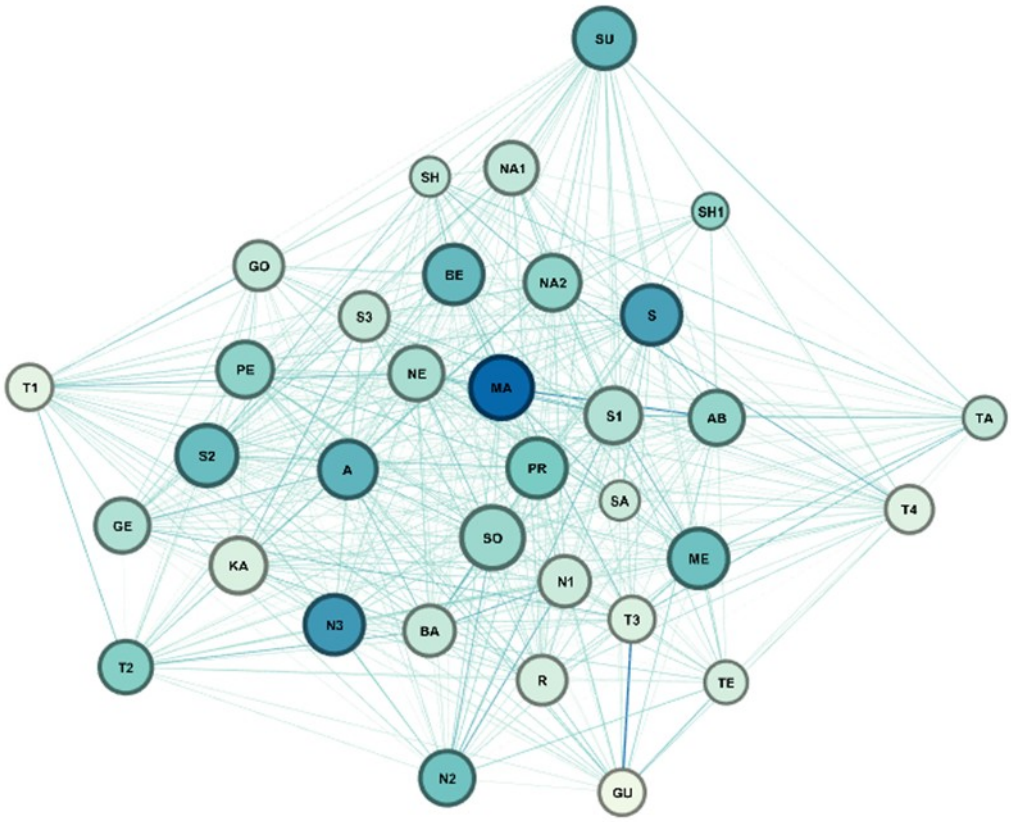


Figure 2.2. Weighted grooming network of Central Himalayan langur female. Networks were built using Gephi 0.9.2 beta [Cherven, 2013]. A node (circle) size represents the individual's degree centrality (higher centrality, larger the size of the node). A node (circle) color represent the rank of the individual (higher the rank, stronger is the color of the node). Node label

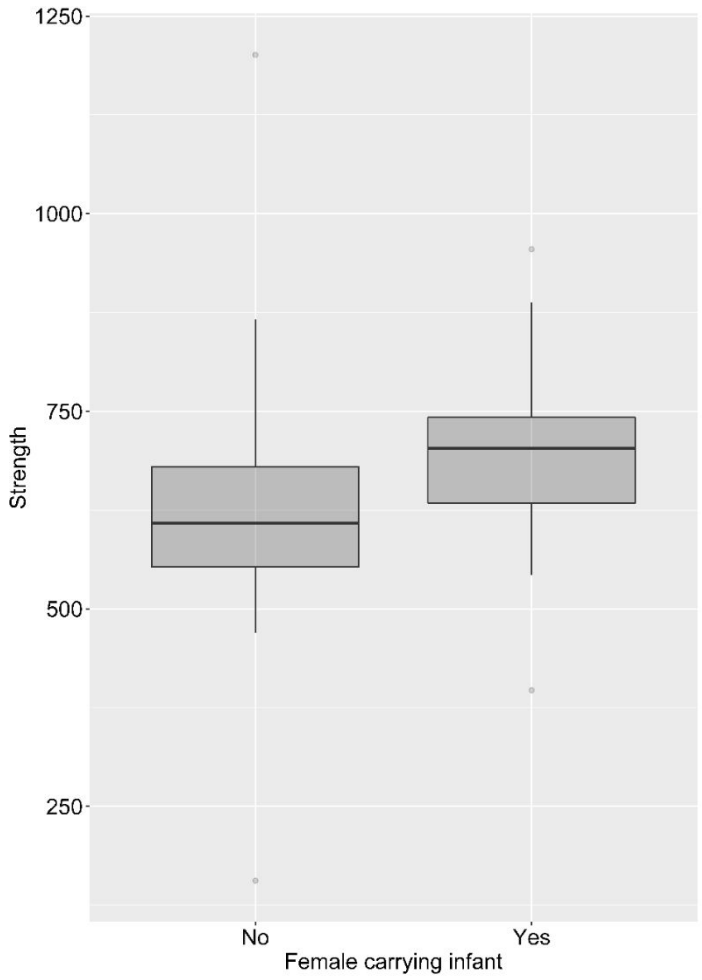


Figure 2.3. Strength centrality of Central Himalayan langur female in relation to infant status. The box bounds the IQR (equal distance between first and third quartiles) divided by the median while the whiskers extend to a maximum of 1.5 × IQR beyond the box.

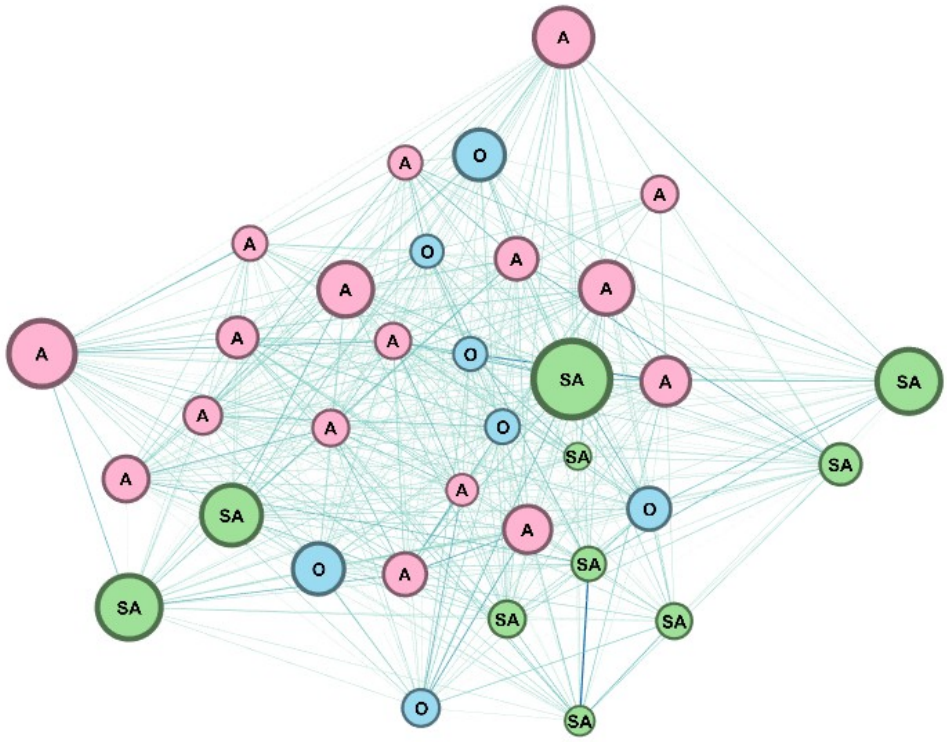


Figure 2.4. Weighted grooming network of Central Himalayan langur female. Networks were built using Gephi 0.9.2 beta [Cherven, 2013]. A node (circle) size represents the individual's betweenness centrality (higher centrality, larger the size of the node). A node (circle) color represent the age classification, A: adult female, SA: subadult female, O: old female.

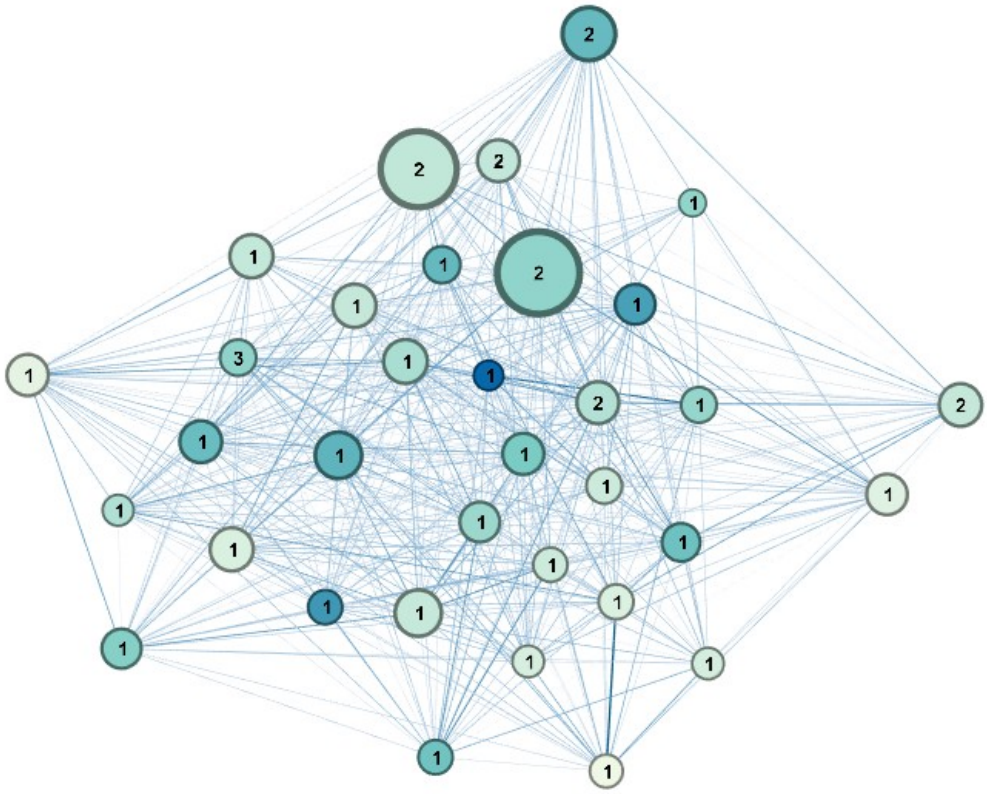


Figure 2.5. Weighted grooming network of Central Himalayan langur female. Networks were built using Gephi 0.9.2 beta [Cherven, 2013]. A node (circle) size represents the individual's eigenvector centrality (higher centrality, larger the size of the node). A node (circle) color represent the rank of the individual (higher the rank, stronger is the color of the node). Node symbol represent the mtDNA haplotypes, 1: type 1 haplotype, 2: type 2 haplotype, 3: type 3

2.5. Discussion

This study found that females with the strongest direct connections were high-ranking females who had a greater number of grooming partners and females with infants had the strongest bond. However, sub-adult and immigrant females have strong indirect connections. Sub-adult females connected more with females who do not interact with one another and immigrant females formed strong grooming relationships with females who themselves had strong bonds.

There is growing evidence from a variety of primate species that dominance provides fitness benefit (Majolo et al., 2012). In the Northern Plains Sacred Langur, high ranking females have high reproductive success (Borries et al., 1991; Borries, 1993) and strong grooming bonds (Borries et al., 1994). However, my study shows that high ranking CHL females have a greater number of social partners (high degree), but do not form stronger bonds. 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 and Majolo, 2013). Many social animals living in cold environments form groupings of individuals to keep warm by minimizing their heat loss (Gilbert et al., 2010). Therefore, primate species inhabiting extreme cold climates could gain fitness benefit from forming more social bonds. For example, barbary macaques with more grooming partners form larger huddles and experience grater probability of winter survival (Campbell et al., 2018). Japanese macaque (*Macaca fuscata*) high ranking males also form larger huddling groups with other kin during cold winter nights (Takahashi, 1997). I did not collect data during the peak of winter (December to March), but my previous study on the same group showed a high rate of huddling in winter (Nautiyal, 2015). It might be possible, that CHL high-ranking females invest to form social relationships with many females rather then forming strong social bonds with a few females, to help survive cold winters, giving high ranking females more opportunity to join huddling groups.

Compared to females without a dependent infant, females with infants formed strong bonds, but did not have a greater number of social partners. For females who are carrying a young infant, forming strong social bonds could provide a higher chance of infant survival (Silk et al., 2003). Several factors can explain the connection between female sociality and reproductive success, such as protection from predation. Females with stronger and more

secure social bonds may be less spatially peripheral, particularly when they are feeding during the day and when sitting in sleeping trees at night (Silk et al., 2009). Dog predation is high in this site and the primary case of infant and juvenile mortality (Nautiyal et al, in prep; Chapter 5). Also the group often feeds inside the agricultural land (Nautiyal et al., 2020; Chapter 4), where they are most vulnerable to attack by dogs. Dogs killed three adult females during the study. Females living in such habitats can gain advantages from strong social bonds with other females and that may enhance infant survival. Alternatively, females may be getting more grooming in exchange for passing their infants to females intensely interested in holding them (Muroyama, 1994). Interactions between newborn infants and other group members are quite common in hanuman langur species (Hardy, 1977). Maintaining such strong relationships with allomothers could also contribute to an infant's survival if the biological mother dies. Orphaned infants sometimes are adopted by allomothers (Kohda, 1985)

Primates are known to demonstrate an understanding of third party relationships (Brent et al., 2014; Cheney, 2011). CHL sub-adult females occupied network positions with a high level of influence (high betweenness) and groomed with females who do not interact with each other. As such, individuals with high betweenness may obtain fitness benefits with these indirect connections. In male chimpanzees, high betweenness predicted a rise in rank and offspring siring (Gilby et al., 2013). CHL sub-adult females had comparatively lower rank than adult and old females (Table 1). Sub-adult females made more indirect connections with other group members, such as grooming with 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 sub-adult 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. Therefore it is possible that subadult females' indirect connections may help to facilitate their rise in rank in the future, which in turn could be directly linked to future reproductive success.

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, indirect connections (betweenness and eigenvector) have been shown to display significant heritability (Brent et al., 2013). In this study, I found that females who have mtDNA haplotype 2 had 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 were considered to be immigrants. This highlights the possibility that indirect connections are not heritable in CHL. This suggest a behavioral strategy whereby immigrant females having strong social bonds with their limited number of close kin, may also have strong bonds with many natal females who have the most central positions in the network. One could imagine that immigrant females either attain peripheral positions in the group or reach high-ranking positions after displacing dominant females.

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). 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.

Female CHL exhibit a high degree of behavioral flexibility, influencing their position in the group's social network, with potentially important consequences for their survival in a high-altitude human dominated landscape. In particular, future research is needed to follow the long-term consequences of the behavioral strategies of young females on the survival and fitness of their offspring.

Table 2.1. Sample information of Central Himalayan langur (*Semnopithecus schistaceus*) females used in mtDNA sequencing (n= 29). Three mtDNA regions, the control region (CR), cytochrome b (CYTB) gene and the 1.8 kb region, were examined (✓: DNA sequence data available).

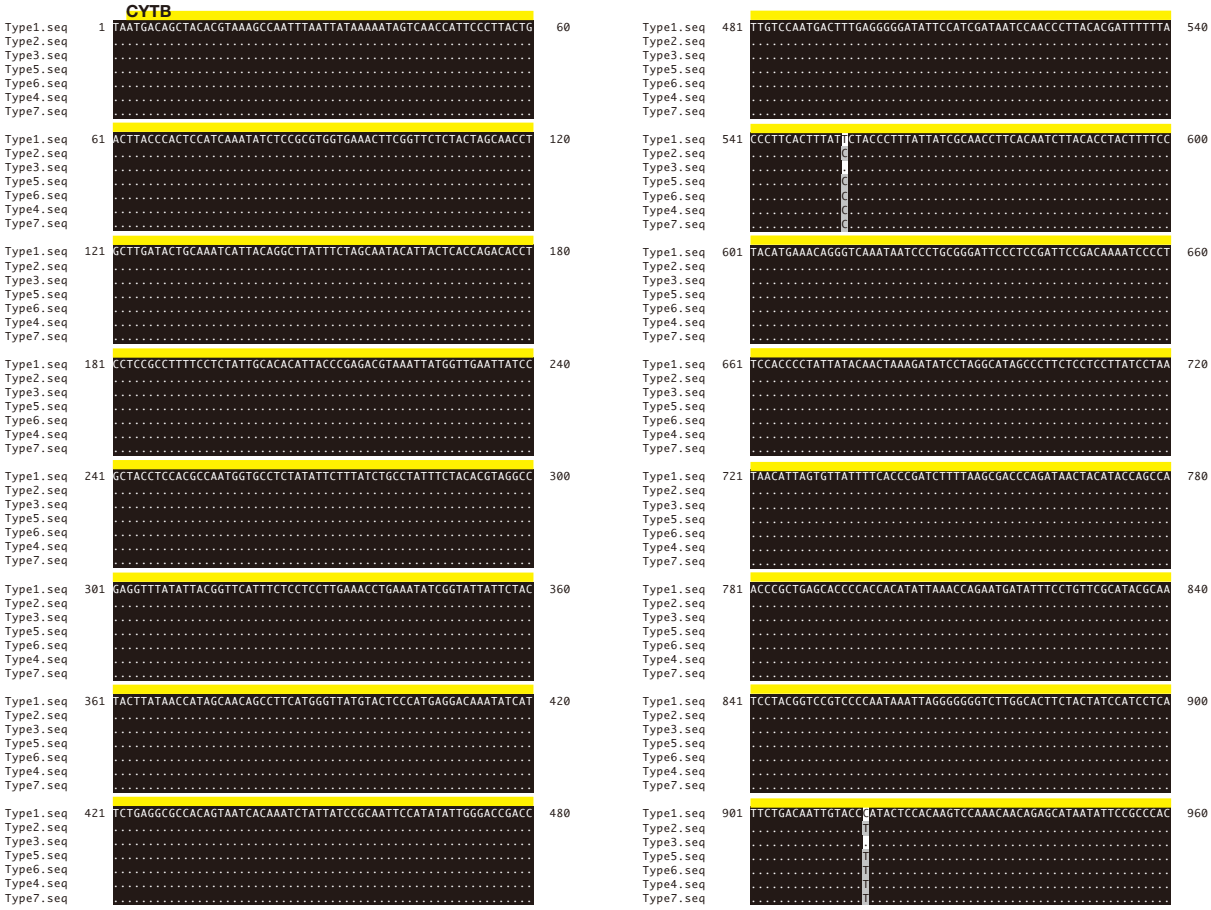
Adult females	ID code	Age/sex	Rank (normalized David score)	Observation hours	MtDNA			MtDNA haplotype
					CR	CYTB	1.8 kb	
Abhi	A	A	18. 3	36	✓	n.e.	n.e.	Type 1
Abhi2	AB	A	16. 74	28	✓	n.e.	n.e.	Type 1
Badi	BA	A	15. 43	30	✓	n.a.	✓	Type 1
Beauty	BE	O	18. 15	30	✓	✓	✓	Type 1
Geeta	GE	A	16. 02	29	✓	✓	✓	Type 1
Goli	GO	A	15. 5	34	✓	n.a.	✓	Type 1
Gulabo	GU	SA	14. 28	31	✓	n.e.	n.e.	Type 1
*Katori	KA	SA	14. 89	29				*Type 1
Manu	MA	O	20. 79	31	✓	n.a.	✓	Type 1
Meenu	ME	O	17. 85	28	✓	n.a.	✓	Type 1
Naina	N1	A	15. 24	28	✓	n.e.	n.e.	Type 1
Nalini1	N2	O	17. 78	15	✓	n.a.	✓	Type 1
Nalini2	N3	O	19. 2	38	✓	n.a.	✓	Type 1
*Nani1	NA1	O	15. 52	26				*Type 2
Nani2	NA2	A	16. 9	34	✓	✓	✓	Type 2
Neelu	NE	A	16. 2	28	✓	n.e.	n.e.	Type 1
Peeli	PE	A	16. 97	33	✓	✓	✓	Type 3
*Pretty	PR	O	17. 53	32				*Type 1
Rohit	R	SA	14. 97	25	✓	n.e.	n.e.	Type 1
Sahas	S	A	18. 95	36	✓	n.a.	✓	Type 1
*Santa	SA	SA	15. 23	26				*Type 1
Sanu1	S1	A	15. 97	28	✓	n.e.	n.e.	Type 2
Sanu2	S2	A	18. 01	31	✓	n.e.	n.e.	Type 1
Sanu3	S3	A	15. 47	27	✓	n.e.	n.e.	Type 1
Shakti	SH	A	15. 57	39	✓	n.e.	n.e.	Type 2
*Sheeta	SH1	A	16. 86	32				*Type 1
Soli	SO	A	16. 6	28	✓	n.e.	n.e.	Type 1
Sukhveer	SU	A	18. 1	31	✓	n.e.	n.e.	Type 2
Taklu	TA	SA	15. 47	12	✓	n.e.	n.e.	Type 2
Tandi	T1	A	14. 57	25	✓	n.e.	n.e.	Type 1
Tandi jr	T2	SA	17. 2	36	✓	n.e.	n.e.	Type 1
Tanisha	T3	SA	14. 84	28	✓	n.e.	n.e.	Type 1
Tashi	T4	SA	14. 72	28	✓	n.e.	n.e.	Type 1
Teenu	TE	SA	15. 01	28	✓	n.e.	n.e.	Type 1

Abbreviation of Age/Sex, A: adult female, SA: sub-adult female, O: old female. n.e: not examined. n.a.: not amplified in PCR, *MtDNA haplotype assigned based on mother-daughter relationship through behavior observation.

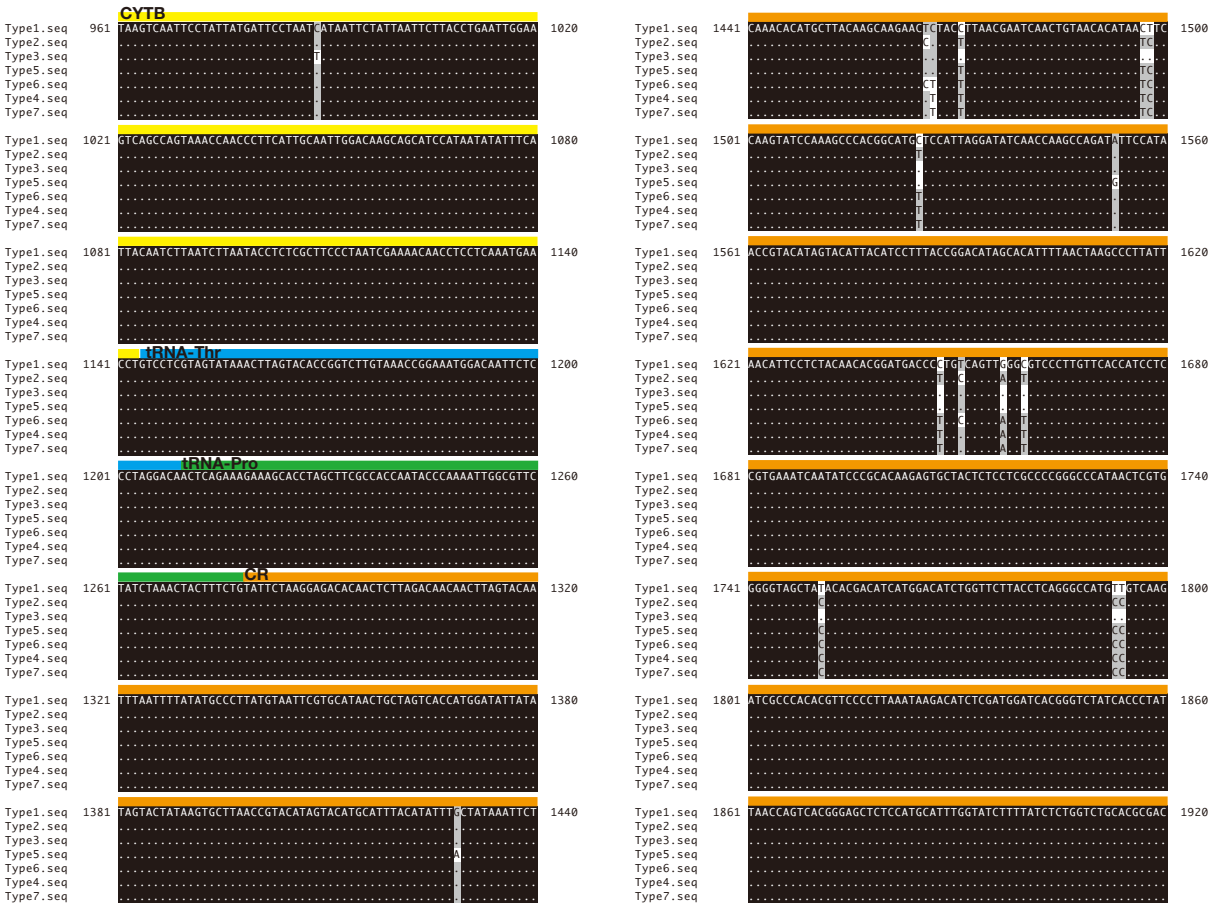
Table 2.2. Parameter estimated from generalized linear models explaining variation in network centrality among Central Himalayan langur females

Centrality coefficients	Predictors	Estimate	SE	z value	p value
Degree	(Intercept)	1.57	6.14	0.256	0.798
	Rank	1.59	0.43	3.772	0.0002***
Strength	(Intercept)	563.42	38.80	14.486	<2e-16***
	Reproductive status	82.84	40.87	2.028	0.143
	Infant status	129.03	47.76	2.702	0.007**
Betweenness	(Intercept)	16.78	3.52	4.772	1.82e-06***
	Genetic relatedness (Type 2)	2.21	6.19	0.357	0.722
	Genetic relatedness (Type 3)	-16.93	9.56	-1.772	0.077
	Age (Old)	6.97	5.99	1.163	0.245
	Age (Young)	12.32	5.35	2.304	0.022*
Eigenvector	(Intercept)	4.40	0.89	5.058	4.24e-07***
	Rank	-0.13	0.07	-1.987	0.048*
	Genetic relatedness (Type 2)	-0.96	0.22	-4.579	4.66e-06***
	Genetic relatedness (Type 3)	0.47	0.42	1.119	0.264
	Infant status	-0.20	0.14	-2.285	0.225

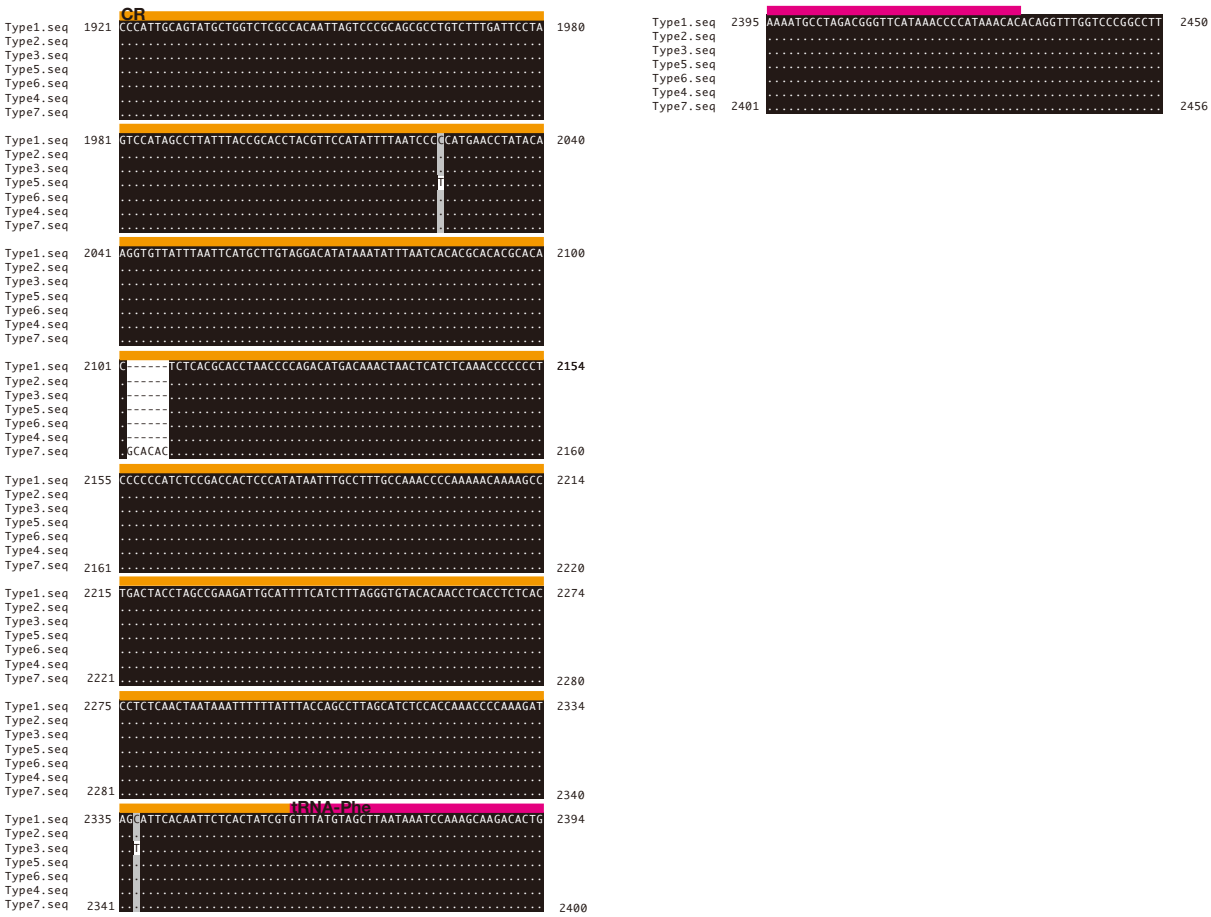
Significant codes are marked as follows: "***" $P< 0.001$, "**" $P< 0.01$, "*" $P<0.05$.



Appendix Figure 2.1. Alignment of 7 mtDNA haplotypes detected in the study group of the Central Himalayan langur (*Semnopithecus schistaceus*). Comparing to Type 1, dot (.) indicates the same nucleotide at each site. Approx. 2.4 kb determined in this study contains cytochrome b (CYTB) gene, tRNA-Thr, tRNA-Pro, the control region (CR = D-loop) and tRNA-Phe, based on the alignment with *Semnopitecus entellus* mtDNA (Genbank accession No.: EU0004478, Osterholz et al., 2008).



Appendix Figure 2.1 (continued).



Appendix Figure 2.1 (continued).

Appendix Table 2.1. Distribution of 7 mtDNA haplotypes in the study group of the Central Himalayan Langur (*Semnopithecus schistaceus*) in age/ sex classes.

Age/sex	MtDNA							Total
	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	
AF	20	4	1	0	0	0	0	25
AM	2	1	1	2	1	1	2	10
SubF	4	1	0	0	0	0	0	5
SubM	6	1	0	0	0	0	0	7
Jv/Inf	6	1	0	0	0	0	0	7
Total	38	8	2	2	1	1	2	54

Abbreviation of age/sex class, AF: adult female, AM: adult male, Sub F: sub-adult female, Sub M: sub-adult male, Jv/Inf: Juvenile and Infant of both sexes

Appendix Table 2.2. *Degree centrality* model characteristics

Models	**K**	**AICc**	**ΔAICc**	**Weight**	**Cum.weight**	**Log-likelihood**
normDS	5	340.15	0.00	0.83	0.83	-164.58
mtDNA-normDS	7	344.61	4.46	0.09	0.92	-164.34
normDS-mtDNA-Infant	8	346.84	6.69	0.03	0.95	-164.16
mtDNA-normDS-Age	8	347.18	7.02	0.02	0.97	-164.32
mtDNA-normDS-Mating	9	348.96	8.80	0.01	0.98	-163.87
Infant-Mating	6	349.70	9.55	0.01	0.99	-168.14
Null	4	350.11	9.95	0.00	0.99	-170.72
normDS-mtDNA-Age-Infant	10	351.53	11.38	0.00	1.00	-163.77
Infant	5	352.44	12.29	0.00	1.00	-170.72
Integrated	11	353.34	13.19	0.00	1.00	-163.23
mtDNA	6	354.33	14.18	0.00	1.00	-170.45
mtDNA-Infant	7	356.82	16.67	0.00	1.00	-170.45

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Aikaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; K: number of variables included; Mating- mating status; mtDNA: mitochondrial haplotypes; normDS: normalized David score ‘rank’; Infant: infant status; Weight: model probabilities

Appendix Table 2.3. *Strength centrality* model characteristics

Models	K	AICc	ΔAICc	Weight	Cum.weight	Log-likelihood
Mating-Infant	6	835.60	0.00	0.17	0.17	-411.09
mtDNA-Infant- normDS	8	835.76	0.16	0.16	0.33	-408.61
normDS-mtDNA	7	836.38	0.78	0.12	0.45	-410.22
mtDNA-infant	7	836.65	1.05	0.10	0.55	-410.36
mtDNA	6	836.72	1.12	0.10	0.65	-411.65
Infant	5	837.07	1.47	0.08	0.73	-413.04
Null	4	837.56	1.97	0.06	0.80	-414.45
normDS-mtDNA-Age	9	837.86	2.26	0.06	0.85	-408.32
normDS	5	838.10	2.50	0.05	0.90	-413.55
Integrated	11	838.88	3.28	0.03	0.93	-405.99
normDS-mtDNA-Infant-Age	10	838.91	3.31	0.03	0.97	-407.46
normDS-mtDNA-Mating	8	838.95	3.35	0.03	1.00	-410.21

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Aikaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; K: number of variables included; Mating- mating status; mtDNA: mitochondrial haplotypes; normDS: normalized David score ‘rank’; Infant: infant status; Weight: model probabilities

Appendix Table 2.4. *Betweenness centrality* model characteristics

Models	K	AICc	ΔAICc	Weight	Cum.weight	Log-likelihood
mtDNA-Age	4	586.92	0.00	0.32	0.32	-289.13
Null	8	588.88	1.95	0.12	0.44	-285.18
Mating-mtDNA-Age	9	588.91	1.98	0.12	0.55	-283.85
mtDNA-normDS-Age	6	589.07	2.15	0.11	0.66	-287.83
Infant	5	589.25	2.32	0.10	0.76	-289.12
normDS-Age	7	589.63	2.70	0.08	0.84	-286.85
normDS-mt DNA-Mating	8	590.21	3.28	0.06	0.90	-285.84
normDS-mtDNA-Age	7	591.46	4.53	0.03	0.94	-287.76
normDS-mtDNA-Age	9	591.56	4.64	0.03	0.97	-285.17
mtDNA-normDS-Age-Infant	10	593.47	6.54	0.01	0.98	-284.73
Integrated	11	593.66	6.74	0.01	0.99	-283.39
mtDNA-Infant-normDS	8	594.03	7.11	0.01	1.00	-287.75

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Aikaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; K: number of variables included; Mating- mating status; mtDNA: mitochondrial haplotypes; normDS: normalized David score 'rank'; Infant: infant status; Weight: model probabilities.

Appendix Table 2.5. *Eigenvector centrality* model characteristics

Models	K	AICc	ΔAICc	Weight	Cum.weight	Log-likelihood
normDS-mtDNA-Infant	8	-106.84	0.00	0.39	0.39	62.68
mtDNA-Infant	7	-105.59	1.25	0.21	0.60	60.76
normDS-mtDNA	7	-104.49	2.35	0.12	0.72	60.21
mtDNA	6	-104.45	2.39	0.12	0.84	58.94
normDS-mtDNA-Mating	8	-102.88	3.96	0.12	0.89	60.70
normDS-mtDNA-Infant-Age	10	-102.51	4.33	0.05	0.94	63.25
normDS-mtDNA-Age	9	-101.79	5.05	0.04	0.97	61.50
Integrated	11	-101.52	5.32	0.03	1.00	64.21
Mating-Infant	6	-95.59	11.25	0.00	1.00	54.51
Infant	5	-95.33	11.51	0.00	1.00	53.16
Null	4	-93.8	13.04	0.00	1.00	51.23
normDS	5	-92.92	13.92	0.00	1.00	51.96

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Aikaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; K: number of variables included; Mating- mating status; mtDNA: mitochondrial haplotypes; normDS: normalized David score ‘rank’; Infant: infant status; Weight: model probabilities.

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CHAPTER 3

THE BANJ OAK *Quercus leucotrichophora* AS A POTENTIAL MITIGATING FACTOR FOR HUMAN-LANGUR INTERACTIONS IN THE GARHWAL HIMALAYAS, INDIA: PEOPLE'S PERCEPTIONS AND ECOLOGICAL IMPORTANCE

Photo credits: Himani Nautiyal

Chapter 3

The Banj oak *Quercus leucotrichophora* as a potential mitigating factor for human-langur interactions in the Garhwal Himalayas, India: people's perceptions and ecological importance

3.1. Abstract

Crop-foraging by primates is a rapidly growing concern. Effective mitigation strategies are urgently required to resolve this issue. In the Garhwal Himalayas, local people's high dependency on forest resources is a major cause of habitat loss, which paves the way for human-primate interactions in this area. To investigate the socioeconomic factors that might explain langur crop-foraging, we conducted structured interviews among 215 households in the Garhwal Himalayas India. We also examined langur resource use by monitoring their feeding and sleeping site activity. Less agricultural land, less agricultural production, and possession of large numbers of livestock significantly predicted villagers reporting crop-foraging events, although economic status of the correspondents did not have any effect. Perception of the villagers about reduction in forest resource was significantly affected by the amount of livestock possessed by the villagers. Our observations suggested that Banj oak *Quercus leucotrichophora* was the dominant species (59.2%, N = 306) in the pool of sleeping trees used by the langurs. Langurs also showed a preference in their use of sleeping sites and feeding sites, which were different from that expected by chance. Sleeping sites with high density of oak were re-used most frequently. Similarly, dense oak patches were also the preferred feeding patches. Thus, we suggest replanting of oak trees and conservation of intact oak patches, environmental education outreach, and empowerment of women in the community as potential mitigating factors to lessen the interaction between humans and langurs.

3.2. Introduction

Interactions between people and wildlife range from mutually beneficial or benign to harmful for one or both parties. These negative interactions are frequently referred to as "human-wildlife conflict" (Wich and Marshall, 2016). Human-wildlife conflict is a rapidly growing concern in today's world across many regions, and manifests itself in forms such as livestock-

loss by predation or crop-foraging by a number of wildlife species (Dickman, 2010). These concerns also have negative consequences for wildlife, resulting in population displacement, harassment or even eradication (Strum, 1987; Else, 1991). While many wildlife species forage on cultivated crops, primates, given their high cognitive abilities, pose an even more significant threat, often thwarting attempts to effectively deter them (i.e. Naughton-Treves, 1998; Sillero-Zubiri and Switzer, 2001; Warren et al., 2007; Nijman and Nekaris, 2010). In Africa and Asia, conflict is high between farmers and crop-foraging wildlife (Hill and Wallace, 2012). Primates alone are responsible for crop-losses of up to 70% on any single farm (Priston, 2005) and often 60% of the annual harvest (Hill, 2000). Effective mitigation strategies are urgently required to resolve this issue and to take suitable conservation actions (Breitenmoser et al., 2005). For predicting the likely success of a crop-foraging prevention model, however, it is crucial to understand the behavioral ecology of the crop-foraging species and local peoples' perceptions of them (Deker and Chase, 1997; Hill et al., 2002; Tadesse and Teketay, 2017). Such models provide a useful framework to explore human-primate interactions and help in the development of effective management plans and conflict-mitigation strategies (Hill and Webber, 2010).

In this paper, we address the problems associated with anthropogenic pressures on the habitat of the Central Himalayan langur (CHL) *Semnopithecus schistaceus*, a rarely studied, montane colobine primate, and the negative consequences arising due to habitat loss around a human-modified landscape in the Garhwal Himalaya of northern India. The Garhwal Himalayas, extending through a major part of the state of Uttarakhand, is an economically underdeveloped and ecologically fragile region of the country, with more than 74% of its population dependent on traditional agricultural practices for their livelihood (Sati, 2012). Anthropogenic pressure is reported to be one of the most significant factors causing deforestation in the Indian Himalayas (FSI, 2000; Pandit et al., 2007; Wester et al., 2019) and it is particularly high in the Garhwal Himalayas (Wakeel et al., 2005; Thakur et al., 2011; Batar et al., 2017), due to low socio-economic status of the local people and their high dependency on natural resources (Bhat et al., 2012). Local people residing in this zone primarily utilize Banj oak *Quercus leucotrichophora* (Troup, 1921; Nautiyal and Babor, 1985). This species covers extensive areas of the central Himalayas, in the altitudinal zone between 500 and 2300 masl (Champion and Seth, 1968; Singh and Singh, 1992; Gairola et al., 2010; Singh et al., 2016). Excessive dependence of the local communities on the oak forests for use as grazing lands, removal of branches for fodder and fuelwood, litter removal for use as cattle beds and as agricultural fertilizer have severely affected the regeneration of this species, having a major inluence on

forest degradation (Gupta and Singh, 1962; Saxena and Srivastava, 1973; Singh and Singh, 1987; Chandra et al., 1989; Singh and Singh, 1992; Thandani and Ashton, 1995; Khera et al., 2001; Rao and Pant, 2001; Arya et al., 2011; Makino, 2011; Rathore et al., 2018).

In general, the oaks are well known for their numerous ecosystem services in the Himalayas. These include conservation of soil from erosion and landslides, regulation of water flow in watersheds and maintenance of water quality in streams and rivers, (Singh and Singh, 1986; Singh et al., 2012). However, they also serve as a major component of the natural habitat and as a key food resource for the wildlife in the region (Singh, 1981; Singh et al., 2012; Nautiyal and Huffman, 2018). To what degree these changes in the oak dominated forest affect the ecology and behavior of the wildlife inhabiting this landscape, is an emerging research topic with important implications for the formulation of wildlife management and conservation strategies.

A study of the diet of a troop of CHL in the Garhwal Himalayas found that their main food source was oak during the fruiting season, but also that 22% of their feeding time was spent on cultivated crops around harvest time (Nautiyal, 2015). To better frame a human-langur conflict-mitigation strategy for this particular landscape, it is important to understand the peoples' perception of langur crop-foraging and to obtain a more detailed picture of langur habitat resource use by monitoring their feeding and sleeping site activity.

This study quantifies the loss of a key tree species, the Banj oak, and its relevance for CHL habitat use. We examined the services provided by oak patches as feeding and sleeping sites for the study langur population and quantified their usage of these oak patches as resource sites. Langurs are diurnal and tend to sleep perched high up on trees during the night. The role of sleeping sites has been assessed under various non-mutually exclusive hypotheses (for a comprehensive review, see Anderson, 1998; Anderson, 2000), particularly given the fact that sleep tends to take up to one third of our lifetime (Purves, 2012). As the highland species of langurs depend heavily on arboreal roosting sites, changes in forest cover and habitat, and a decline in the density of preferable tree species would mean a decrease of suitable sleeping sites as well as of feeding patches, all of which will adversely affect the ecology and ranging behavior of these langurs (Ruhiyat, 1983; Chhangani and Mohnot, 2006).

Langurs (*Semnopithecus* spp.) are one of the most widely distributed primate taxa in the Indian

subcontinent, inhabiting a variety of habitats, ranging from desert to rainforest, from sea level up to 4000 masl in the Himalaya (see Kumar, 1987). Although there have been extensive studies on the lowland langur *S. entellus* (Jay 1963; Jay 1965; Sugiyama 1965; Yoshiba 1967; Mohnot 1971; Hrdy 1974; Newton 1992), there is little information on the ecology, behavior and conservation status of the higher-altitude Himalayan species within this group (Bishop and Bishop, 1978; Sayers and Norconk, 2008). In particular, there is scant information on the behavior and ecology of the CHL, *S. schistaceus* living at high altitudes (Sugiyama, 1976; but see Borries et al., 2015 for lowland dwelling *S. schistaceus*). CITES and IUCN present contradictory information on the conservation status of the species, perhaps due largely to the fact that both are based on scant, unpublished information. To the best of our knowledge, no detailed account of human-langur conflict has been published in India. Leaving the conservation status of *S. schistaceus* unclear, CITES classifies this species in Appendix I as 'Threatened with Extinction' while IUCN ranks it as 'Least Concern' (IUCN Red List, 2015). For merely listed as a subspecies of the widely distributed *Presbytis entellus*, it does appear that very little information actually exists on this newly revised species within its currently recognized high-altitude distribution, across northwest Pakistan, northern India, including the states of Jammu and Kashmir, Himachal Pradesh, Uttarakhand, West Bengal and Sikkim, Nepal, Western Bhutan and the valleys of the Xizang Autonomous Region in southern China (Roos et al., 2014).

This is possibly the first study anywhere to investigate the factors responsible for crop-foraging by any high-altitude langur species and suggest important steps for the mitigation of conflict over resources between langurs and humans, with implications for other nonhuman species residing in and sharing resources with people across the Himalayan landscape. Such a study is likely to be critical to understand human-nonhuman primate interactions inhabiting fragile Himalayan ecosystem for the betterment of both species.

In this context, our paper aims to: (a) provide a langur crop-foraging model with the help of socioeconomic factors as explanatory variables, (b) investigate farmer perceptions of forest loss in the past few decades in relation to habitat loss and crop-foraging by langurs, and (c) evaluate the relationship between Banj oak patch density and its use as langur feeding and sleeping sites.

3.3. Materials and methods

3.3.1 Study site

This study was conducted in the Mandal valley, Chamoli district of Uttarakhand state in the Central Himalayas of India, at an altitude range between 1500 masl–1800 masl (Sharma et al., 2009; Figure 3.1). The Mandal valley has five villages, namely Gondy (G), Kunkuli (KU), Khalla (KH), Mandal (M) and Siroli (SI). The home ranges of two langur troops, S and K, lay within the study site. Troop S's home range covered Gondy, Siroli and Kunkil villages, while Troop K's home range included the Mandal and Khalla villages. The mean average temperature (± SE) of the study site ranges from a maximum of 16.41 (± 3.60) ℃ to a minimum of 6.14 (± 1.98) ℃. The mean annual rainfall is typically 2044.47 ± 476.01 mm (State Forest Department climate data for 1988~2005, cited in Sharma et al. 2009). The socioeconomic conditions and agricultural practices of the valley have been described in detail by Sharma et al. (2009) and Iqbal et al. (2014).

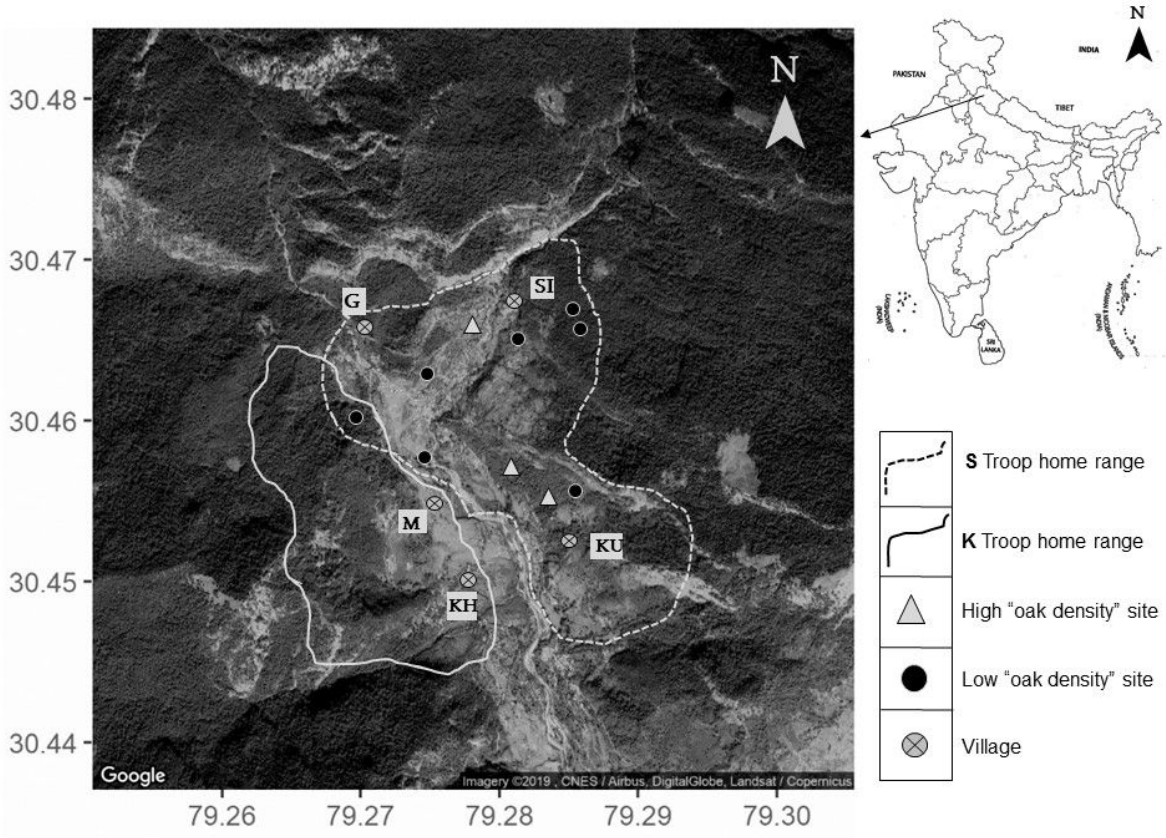

Figure 3.1. Map of the study area, estimated home ranges of Troop S and K, the study villages and the Troop S sleeping sites

3.3.2. Questionnaire data

A total of 215 households, comprising > 90% of all households, from the five study villages were surveyed between October and December 2015 (Table 3.2). A structured questionnaire was given to one adult member of each household surveyed. Whenever possible, the adult woman of the household was given the questionnaire, as they appeared to have more accurate knowledge of the forest and agricultural fields, being responsible for most work done in the fields. The questionnaire was divided into three parts: Socioeconomics, crop damage by langurs and people's perception about reduction of forest resources.

3.3.3. Sleeping site and feeding patch use data

Sleeping site and feeding patch data collection took place between August and December 2018 on Troop S. Although we had identified two troops, K and S, in the Mandal valley, we focused on the already habituated Troop S, for this part of this study. The troop ranged over an area of 2 km^2. We also selected Troop S because a maximum of respondents (85% from village SI and 100% from village KU) from this troop's home range reported crop-foraging by langurs (Figure 3.1). The members of this troop lived in a multi-male multi-female social group, comprising 78 individuals that included eight adult males, 32 adult females, seven subadult males, nine subadult females and 22 infant and juvenile males and females.

We recorded the location of langur sleeping sites, the tree species and feeding patch sites used to quantify habitat use patterns and to assess the relative value of different resources to the langurs. Sleeping site occupancy was recorded for 112 nights from August to December 2018. The troop was located in the early hours before sunrise at the sleeping site and was followed until the next sleeping site in the evening. The troop members typically spread out and occupied more than one tree to sleep on each evening. To keep track of this usage, every single tree that was used at least once at a sleeping site was identified to species level and marked with an alphabetical code for re-identification. Tree re-use was then scored to quantify sleeping tree species preferences. Each re-used tree had a total score greater than zero while a tree that was used only once had a re-use score of zero.

Direct and indirect methods were both used to determine sleeping sites. In the direct method, a troop was followed to the sleeping site and location was confirmed once the troop settled

down at that particular site. The indirect sleeping site confirmation method, as has been employed for other primates, involved the finding of fresh fecal material under and around particular trees the next morning (Liu and Zhao, 2004; Cui et al., 2006; Stewart and Pruetz, 2013).

A feeding patch was defined as a locality that was utilized by langurs for their feeding activities for a period of at least 30 min. Feeding patches were identified during whole-day follows of the troop (N = 115 days, from August to December 2018). All individual feeding patches visited over a single day were coded according to their nearest sleeping site to quantify habitat-use patterns. On some occasions, the feeding patches were located near more than one sleeping site. For observations of feeding behavior, we conducted 20-min scan sampling sessions at 10-minute intervals (Altmann, 1974). We followed the troop for a total of 1035 h, with comparable hours of observation spent each month during the study period. A hand-held GPS (Garmin GPSMAP 62s, Garmin, Olathe, Kansas, USA) was used to mark the locations of the langur sleeping sites and feeding patches recorded during the study.

3.3.4. Vegetation data

We used the Point-Centered Quartered Method (PCQM) (see Mitchell, 2010) to estimate oak tree density at each sleeping site. PCQM was first developed by Stearns (1949), then evaluated through a comparison of different methods by Cottam and Curtis (1956). It is an efficient and economic plot-less method that has also been shown to be flexible across sample sizes (Cottam and Curtis, 1956), while causing minimal damage to the understory of the forest (Cunningham, 2001). We established 30-m line transects in the vicinity of the langur sleeping and feeding sites and recorded our data at 10-m intervals to avoid the possibility of repeating bias. At the points where measurements were taken, we drew a line perpendicular to the transect line to generate four quarters and measured the nearest tree in each of these four quarters. Although ideally no limit should be set for the "nearest" tree, we set a limit of 30 m (equal to one transect length) while identifying the nearest tree.

3.3.5. Statistical analysis

We built generalized linear mixed-effect models (GLMM) to analyze people's responses to our questionnaire regarding crop-foraging by langurs and reduction in forest resources surrounding

the study villages. For the first model, we used people's perceptions of crop-foraging by langurs ('Present' or 'Absent') while the second model used people's perceptions of loss of forest vegetation in village forests ('Agree' or 'Do Not Agree') as binary response variables. In each model, socioeconomic variables such as household income, agricultural landholding, agricultural production and total number of livestock were the predictor variables. We included the total number of interview subjects (one individual from each of the 215 household was interviewed) and the villages as control variables. We specified each model with a binomial error structure and logit-link function using maximum-likelihood estimation with the package *lme4* (Bates et al., 2015) in R, version 3.5.2 (R Core Team 2018). In R, we ran tests for homogeneity of residuals and variance inflation factors (VIF) below of around 1 (Field et al 2012). We used an information theory approach based on Akaike's information criterion (IT-AIC) for model selection (i.e., variable selection) to extract the best model to explain human-langur interaction (Burnham and Anderson 2002). The principle of this approach relies on ranking of the model from the candidate set of models based on smallest AIC value (Burnham and Anderson 2002). Using the "aictab function from the package AICcmodavg, we extracted the AIC value for each statistical model separately and then performed model comparisons (Mazerolle, 2016). This function also measures the model's Akaike's weight, or relative likelihood, and accumulative weight of each model that indicates the extent to which one model is more likely than another in explaining the variance in the data. The model characteristics are presented in Table 3.1. For both models, we first compared the full model with interactions between the socioeconomic factors with that without any interaction. We retained the model with the interactions if it outperformed the model without them and then tested it against the null model, which contained only the intercept term. Alternatively, we carried out the same procedure for a model without interactions using the likelihood ratio test (LRT) and the package *lmtest* (Zeileis and Hothorn, 2002).

Sleeping- and feeding patch usage by langurs were assessed using the Poisson parameter. We first generated the frequency distributions of sleeping site re-use (Sokal and Rohlf, 1995; Day and Elwood, 1999) and then tested the differences in expected and observed distributions for the observed frequency range using the Kolmogorov-Smirnov test. P olynomial regression models were used to examine possible relationships between oak tree density and the re-use of sleeping sites and feeding patches. The models were fitted using the '*lm* ()' command in R (James et al., 2013), in order to predict the re-use of sleeping and feeding sites. We used the re-use of sleeping and feeding sites as response variables and oak density as the predictor variable

in both the models. We fitted models up to 5th power of oak density to assess the relationship between usage of sleeping sites and feeding patches, and oak density while maintaining the lower order terms in the equation in each advanced model. We compared the efficiency of these models in explaining the relationship, using Multiple R-Squared value and Residual Standard Error, for the four models. We consecutively compared the four models using the information theory approach based on Akaike's information criterion (IT-AIC) to determine the model with highest explanatory power. The model characteristics are presented in Table 3.4. The fitted quadratic and cubic model coefficients were further used in building the model equations. These equations, now derived from the quadratic and cubic models, were used to simulate the re-use of sleeping sites and feeding patches, in Microsoft Excel. We increased the oak density in step size of 1 to graphically predict the shoot-up point in the re-use of sleeping sites and feeding patches with increasing oak density, and examined whether the re-use values reach an asymptote.

3.4. Results

3.4.1. Demographic, educational and economic characterization of the study villages

The demographic, education and economic details of each of the study villages are shown in Table 3.2. At the time of the study, the total population of Mandal valley was 1,055 people. The mean (± SE) household size was 5.1 (± 0.14) individuals (N = 215 households). Siroli village, with 75 households, was the most populous amongst the villages surveyed. More than 90% of the population in the Mandal valley was educated (up to higher secondary level). The mean monthly income per household across the study villages was INR 14,986 (± 1402 ~ USD 237 ± 23; N = 215), with that of Mandal village being marginally higher than those of the other four villages. Villagers from Mandal and Khalla had more land and a higher annual crop yield, as compared to the other villages. The main crops produced in Mandal valley, like elsewhere in the region, were finger millet *Paspalum scrobiculatum* (*Koda* in Garhwali), barnyard millet *Echinochloa frumentacea* (*Jhangora* in Garhwali), wheat and rice. All of these crops are used only for domestic consumption, as the Himalayan region is unsuitable for large-scale crop production because of the limitations of available space. The annual crop yields varied across the five villages. Siroli village, with its high population, also had more livestock. All households maintained bullocks for plowing the fields and cows for milk. To supplement their income, many households in the valley sold cow and buffalo milk as well. Goats and sheep

were kept for consumption of their meat.

3.4.2. Crop-foraging by langurs in the Mandal valley

Our analysis of langur crop-foraging ('Present' or 'Absent') indicated that the GLMM model with interactions between land characteristics and agricultural production across the landscape did not outperform the corresponding model without any interaction, but did outperform its corresponding null model (LRT; ΔLogLik = 34.99, Δdf = 4, p = 2.3e-14). Our results (Table 3.1) thus indicate that the integrated model with the lowest AICc value of 188 was the best, given the set of eight candidate models, which comprised the variables of landholdings, agricultural production, total number of livestock and income. The economic status of the respondents had no effect on the crop-foraging issues raised by them (GLMM; z = 1.577, p = 0.1150; Table 3.3). Villagers with relatively less cultivated land tended to report more crop-foraging by langurs (GLMM; z = -3.676, p = 0.0003). Agricultural crop production had a significant effect on crop-foraging, with respondents having lower agricultural production reporting relatively higher levels of crop-foraging by langurs (GLMM; z = -2.105, p = 0.0034). Finally, the total number of livestock had a highly significant effect on the villagers' response towards crop-foraging by langurs; those with large livestock holdings reported more crop-foraging (GLMM; z = 4.842, p = 1.29e-06; Figure 3.2).

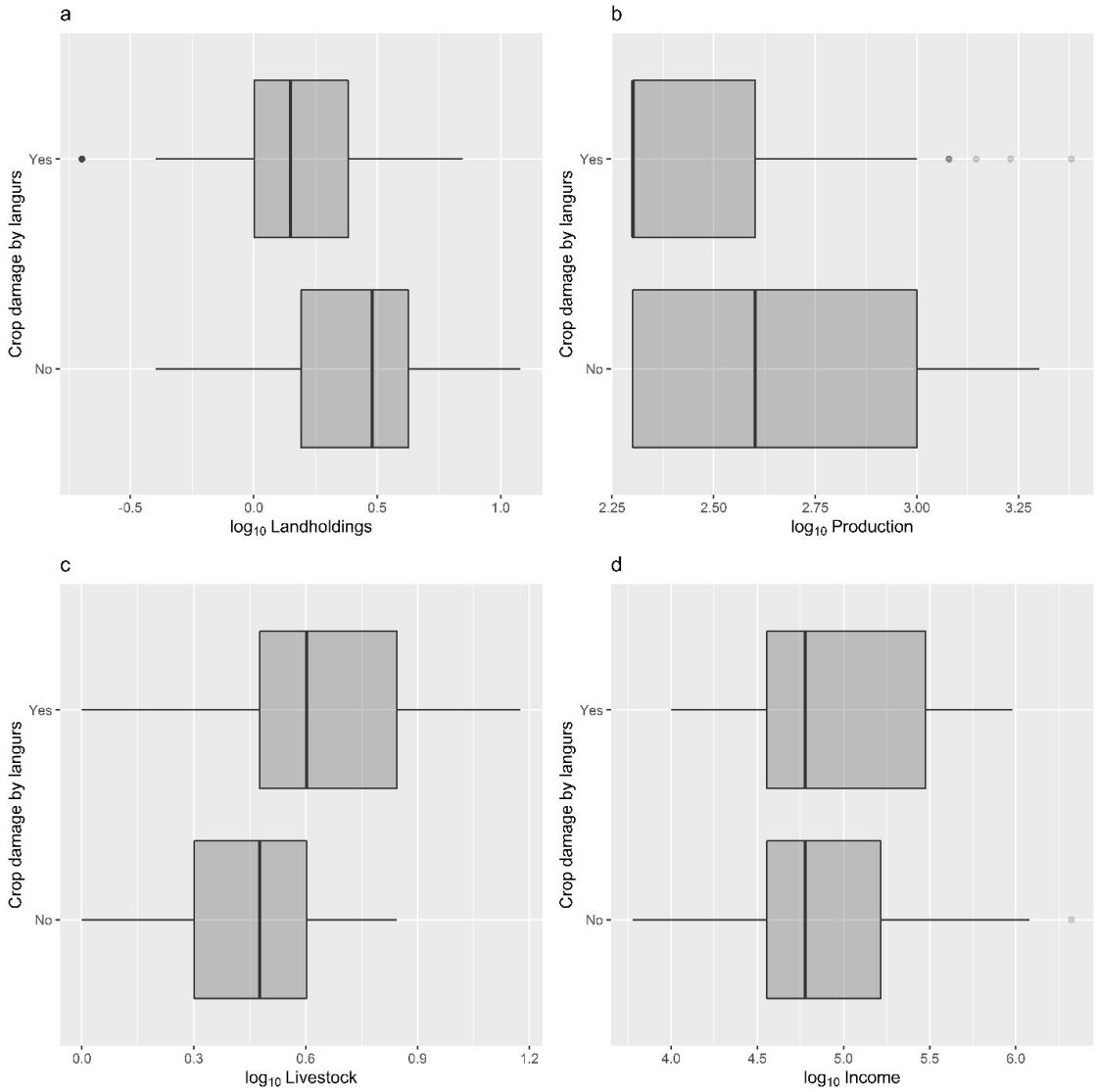

Figure 3.2. Villagers' response to crop damage by langurs in relation to socioeconomic factors (n = 215). Residuals were extracted from generalized linear mixed-effect models (GLMM) with log-number of **(a)** landholdings (ha), **(b)** agricultural production (kg), **(c)** livestock (total number), and **(d)** income per villager (INR) as the predictor variables. The box bounds the IQR (equal distance between first and third quartiles) divided by the median while the whiskers extend to a maximum of 1.5 × IQR beyond the box.

3.4.3. Reduction of forest resources in the Mandal valley

An analysis of perceived reduction of forest resources in the valley revealed that the model with interactions between land characteristics and agricultural production did not outperform the corresponding model without these interactions, but it did perform better than its respective null model (LRT; ΔLogLik = 7.35, Δdf = 4, p = 0.006). The model that combined the variables of landholdings, crop production and total number of livestock had the lowest AICc value of 265 and was the best, given the set of eight candidate models (Table 3.1). The income level of the villagers had no impact on their opinions about forest resource loss in the forests surrounding the villages (Figure 3.3). Farmers' perception of forest resource loss was neither related to total agricultural landholdings (GLMM; z = -1.432, p = 0.1494) nor to agricultural production (GLMM; z = -1.517, p = 0.1293). The total number of livestock holdings, however, had a significant effect on farmers' perception of forest resource loss, with respondents having more livestock reporting a greater degree of resource loss in the village forests (GLMM; z = 2.529, p = 0.0114). Such loss particularly resulted in a perceived decrease of fodder availability, a possible indication of high competition for forest resources among villagers with relatively more livestock (Figure 3.3).

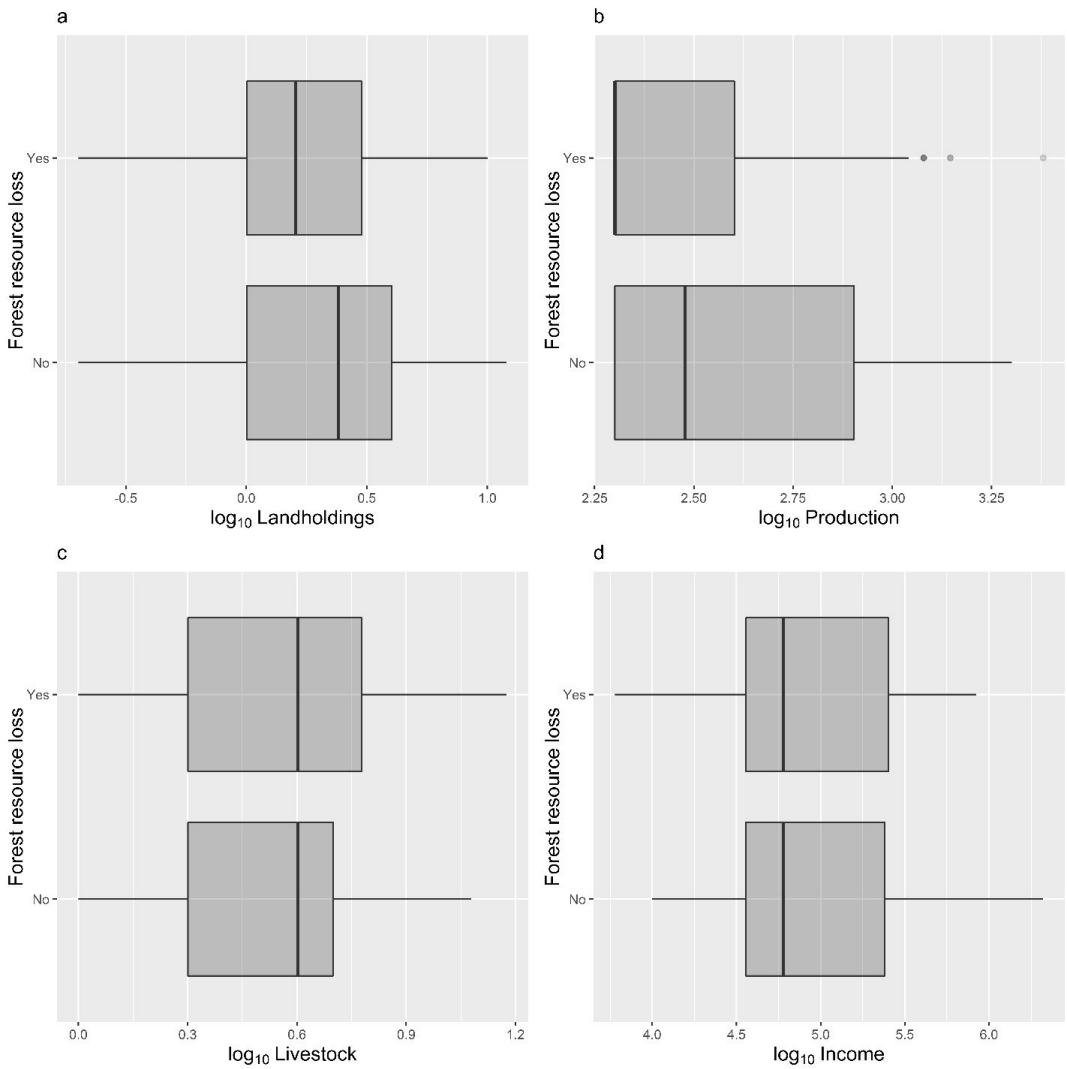

Figure 3.3. Villagers' response to resource loss in neighboring forests in relation to socioeconomic factors (n = 215). Residuals were extracted from generalized linear mixed-effect models (GLMM) with log-number of **(a)** landholdings (ha), **(b)** agricultural production (kg), **(c)** livestock (total number), and **(d)** income per villager (INR) as the predictor variables. The box bounds the IQR (equal distance between first and third quartiles) divided by the median while the whiskers extend to a maximum of 1.5 × IQR beyond the box.

3.4.4. Use of oak as sleeping tree

The study langur troop used a total of 306 unique trees to sleep in, on 96 nights. These trees belonged to 17 different species (Figure 3.4). The troop apparently exhausted their utilization of unique sleeping trees, as an asymptote was reached for the cumulative number of unique sleeping trees over the observation period. The highest represented species in the pool of unique sleeping trees was oak *Quercus leucotrichophora*, with 181 trees (59.15%). The langur troop re-used oak trees periodically (136 times), more than they did all other species combined (88 times) (Chi-square test, $\chi^2 = 10.286$, df = 1, p = 0.0014; Figure 3.4).

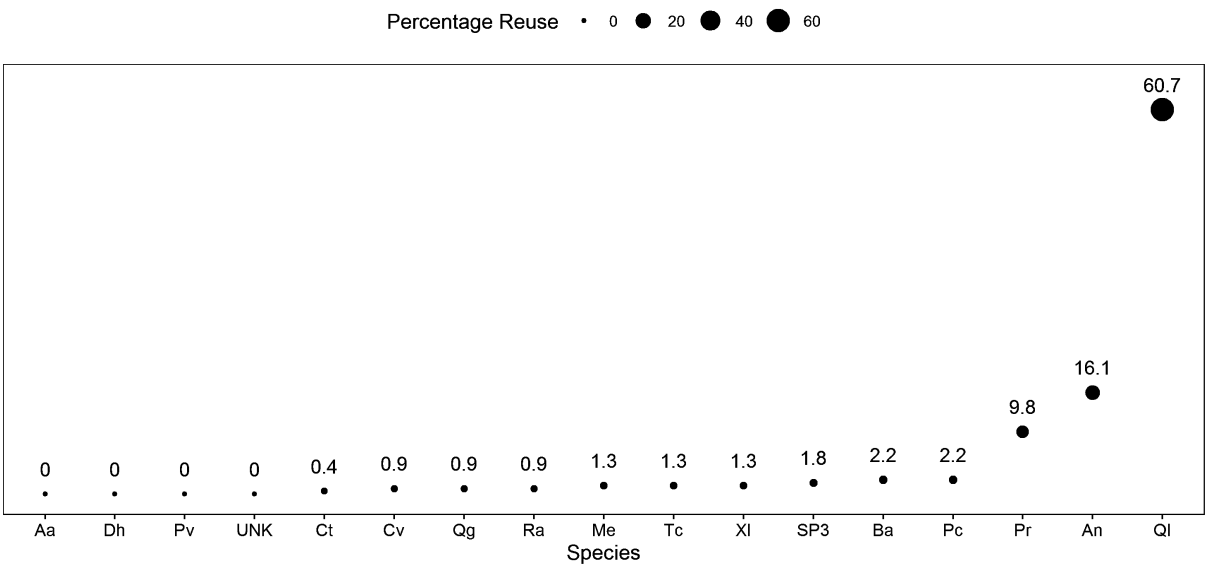

Figure 3.4. Percentage re-use of the 17 recorded tree species, chosen as sleeping trees by the study langur troop. A total of 224 trees were re-used during the study period out of the 306 unique sleeping trees.
Note. Aa – *Ailanthus altissima*, Dh – *Daphniphyllum himalayense*, Pv – *Prunus venosa*, UNK – Undefined species, Ct – *Cupressus torulosa*, Cv – *Carpinus viminea*, Qg – *Quercus glauca*, Ra – *Rhododendron arboreum*, Me – *Myrica esculenta*, Tc – *Toona ciliata*, Xl – *Xylosoma longifolia*, SP3 – Kakaru *(vernacular name. scientific name unavailable)*, Ba – *Betula alnoides*, Pc – *Prunus cerasoides*, Pr – *Pinus roxburghii*, An – *Alnus nepalensis*, Ql – *Quercus leucotrichophora*

3.4.5. Sleeping and feeding site selection

The langurs used 14 sleeping sites, out of which we present vegetation data for 10 sites across 112 observation nights. An asymptote in the cumulative number of sleeping sites was reached after 60 days of observation. Five sleeping sites, constituting approximately 50% of all sites, were used only once or twice, one was used thrice while the remaining sites were used most of the time. The expected number of nights that a troop stayed at each sleeping site was eight (Figure 3.5a). A significant difference between the expected and the observed frequency of usage of sleeping sites was found (Kolmogorov-Smirnov test, $\chi^2 = 0.72727$, p = 5.256e-08; Figure 3.5a). The langurs used some feeding sites more than they did others. On some occasions, the feeding patches were located near more than one sleeping site. We observed 125 instances of usage of a patch as a feeding patch, spread across 14 sleeping sites. On average, 8.92 feeding patches were located adjoining to a sleeping site (Figure 3.5b). The distribution of feeding patches across sleeping sites was significantly different from a random distribution, indicating that there was a preference for feeding in certain areas, as compared to others

(Kolmogorov-Smirnov test, $\chi^2 = 0.65385$, p = 2.98e-05; Figure 3.5b).

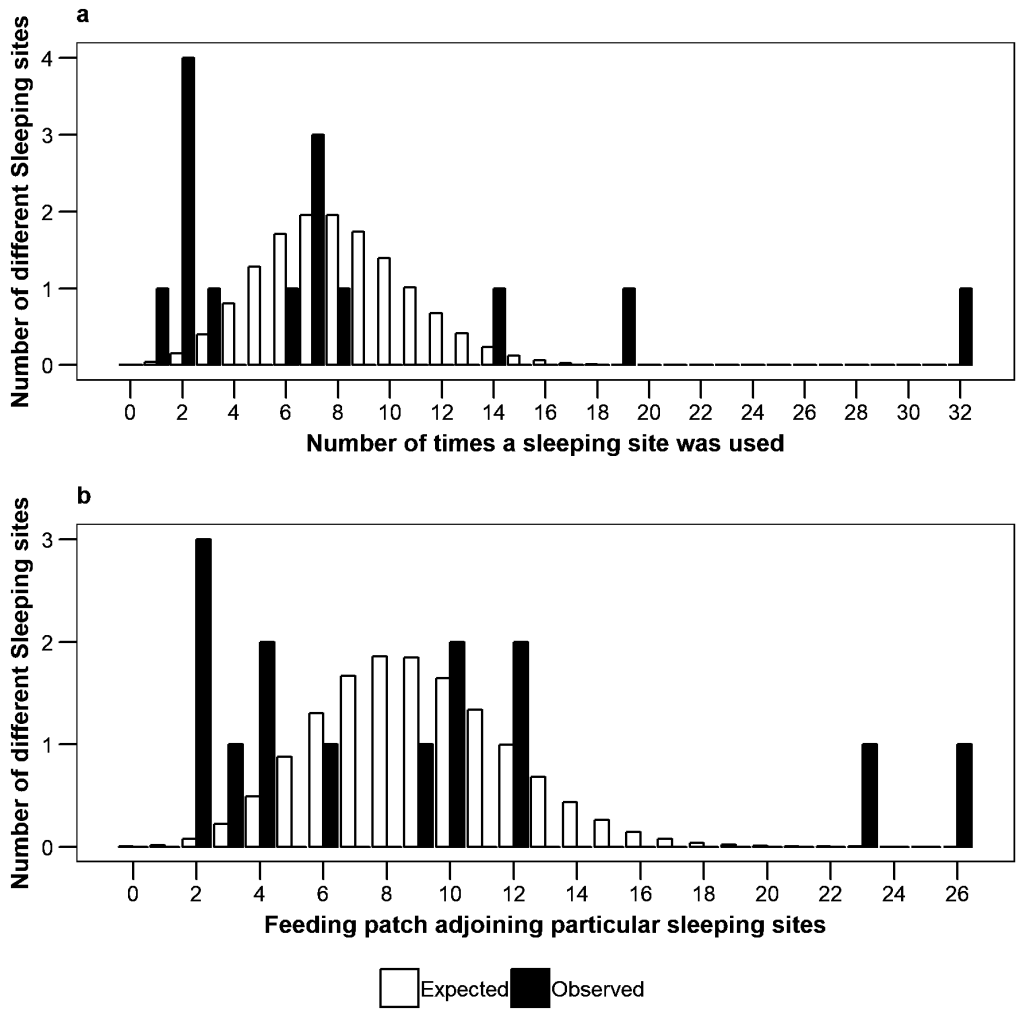

Figure 3.5. Frequency of use of particular sleeping sites and of feeding patches by the study langur troop. The observed and expected values were derived from a Poisson distribution.

3.4.6 Relationship between oak density and habitat use

Sleeping site re-use

The coefficients of both, the quadratic term (t = 2.479, p = 0.0423) and the cubic term (t = 2.627, p = 0.0392) in the polynomial regression models were significant predictors of the usage of sleeping sites. The cubic model differed significantly from the quadratic model (ANOVA; F = 6.612, p = 0.0422) while the higher order models beyond the cubic did not differ significantly from the previous ones (ANOVA; F = 3.096, p = 0.1388). The quadratic model had the lowest AICc value and Akaike weight of 0.66 while the cubic model only differed slightly from the quadratic model in terms of its AICc value (ΔAICc = 1.34, Table 3.4). The quadratic model

explained the usage of sleeping sites better than did the other three models. This relationship showed that the highly dense oak patches were regularly used as a sleeping sites by the langurs. Certain high oak-density sites such as FC (233 trees ha^{-1}), KOP (208 trees ha^{-1}), SROP (207 trees ha^{-1}), in particular, were re-used by the langurs 32 (36.78%), 19 (21.84%) and 14 (16.09%) times respectively during the study. Sites such as MASL, SFI and SFII, where oak was not present, in contrast, were used by the langurs only on one or two occasions (Figure 3.6a). The graphical results from the quadratic regression equation show that up to a certain value of oak density, the usage of oak patches decreased, albeit going into negative values, and then gradually began to increases after a density of 95 trees ha^{-1} (Figure 3.6b).

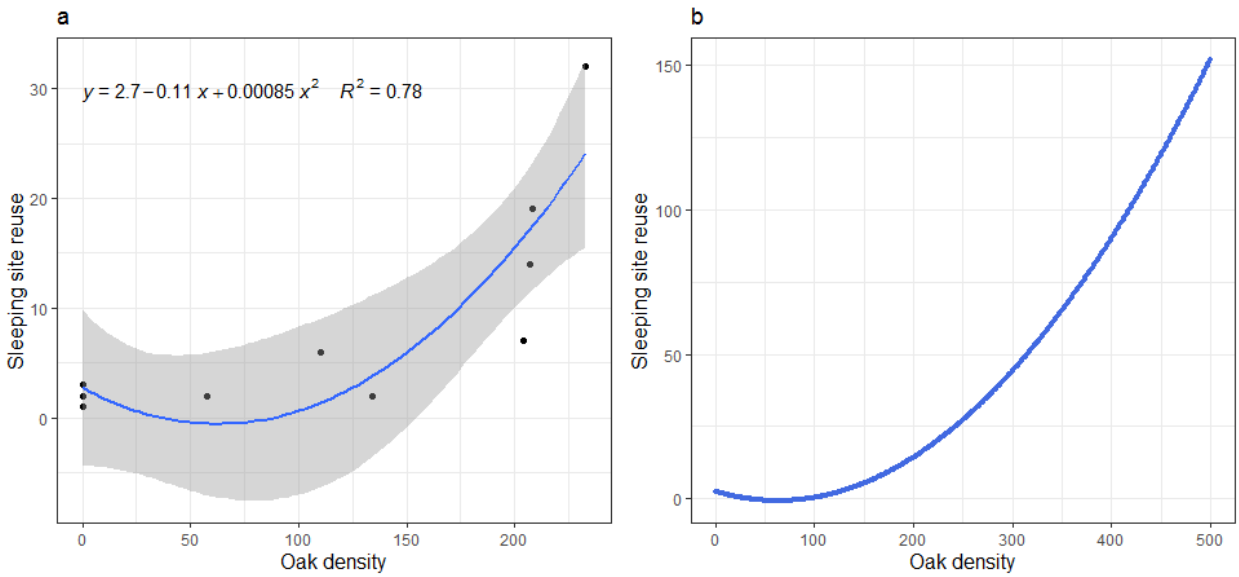

Figure 3.6. Relationship between oak density (trees/ha) and re-use of those locations as sleeping sites, including (a) the observed relationship from 10 sleeping sites, and (b) simulated data derived from the quadratic regression equation.

Feeding site re-use

The quadratic model coefficient was alone a significant predictor of the re-use of feeding patches by the study langurs (t = 1.924, p = 0 .0957) while no other model yielded significant values. The quadratic model had the lowest AICc value with an Akaike weight of 0.98 (Table 3.4). The quadratic model explained the usage of feeding sites better than did the other three models. Oak density did not, therefore, influence the choice of feeding patches as strongly as it governed the choice of sleeping sites (Figure 3.7a). The most frequently visited feeding patches were the top high-density oak patches namely FC, KOP and SROP, which were used by the langurs 41 (26.11%), 47 (29.94%) and 24 (15.29%) times respectively. Vegetation patches with no oak in them, as may be expected, were the least visited sites (Figure 3.6). The

graphical results from the quadratic regression equation shows that the usage of oak patches as feeding patches gradually increased after a density of 192 trees ha^{-1} (Figure 3.7b).

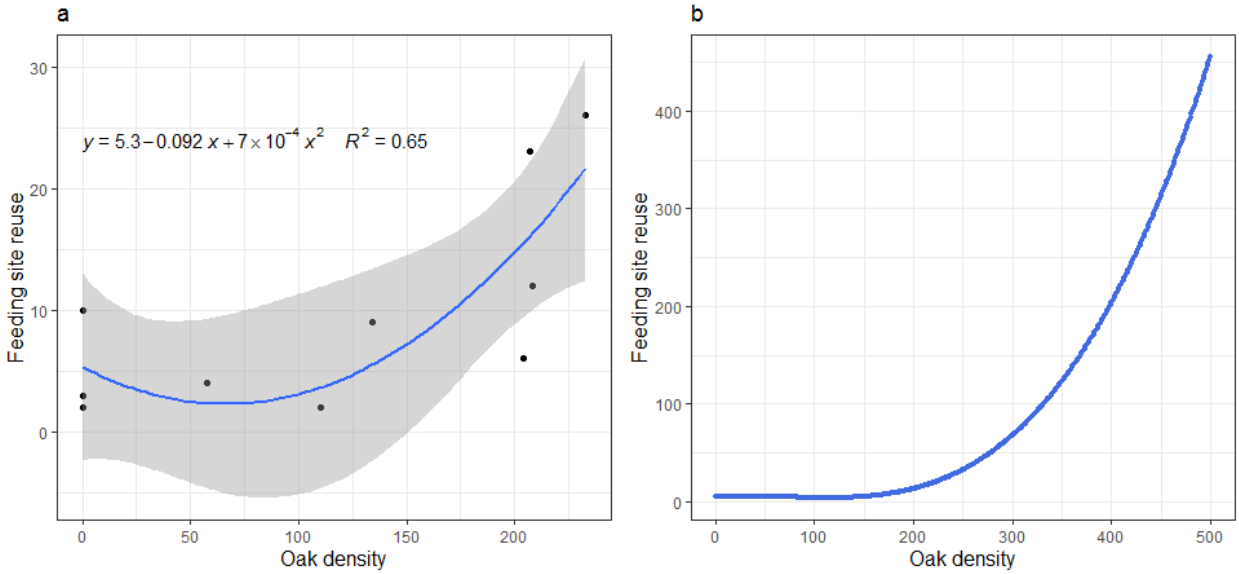

Figure 3.7. Relationship between oak density (trees/ha) and re-use of those locations as feeding sites, including (a) observed relationship from 10 sleeping sites, and (b) simulated data derived from the quadratic regression equation.

3.5. Discussion

3.5.1. Over-exploitation of Banj oak as a potential driver of crop-foraging by langurs

Our results show that villagers, who owned relatively more agricultural land and had good production throughout the whole year, had low interactions with langurs due to their low dependency on natural resources for their livestock. Farmers with relatively less agricultural land and low productivity depended significantly on livestock for extra income and thus relied more on the neighboring forest for grazing their cattle and collecting fodder for them. This high pressure on the surrounding forests is likely to have been a driver for langurs to forage more on agricultural crops in these areas at times of the year when natural food availability in the forest was low. Moreover, respondents who owned a relatively greater number of livestock, as compared to other households, perceived a reduction in the available resources in the nearby forests due to their intensified use of them for livestock fodder. Insufficient crop yields and small cash incomes have typically led households of Mandal valley to depend heavily on forest

resources (Sharma et al., 2009). Based on previous studies by Sharma at al. (2009) and by Singh and Rawat (2012), which investigated three villages in the Mandal valley, Khalla, Siroli and Mandal, the daily fodder consumption per household was observed to be significantly correlated with the number of livestock per household. Hence, we suggest that this increased livestock-driven pressure on the forest compels wild herbivores to compete with livestock for food. This may also help explain the reportedly higher crop damage to households that had more cattle and had their perceptions of significant loss of resources in the village managed forests. Agricultural land, annual crop production and livestock populations thus emerged to be the strongest predictors of crop damage by langurs in the Mandal valley.

Livestock formed an important part of subsistence activities for the human communities in the valley and there appeared to be high competition for forest resources among villagers with more livestock. In particular, the dependence of these communities on the oak forests for fodder, cattle grazing and for fuel wood generated considerable stress on the forests surrounding these villages and appeared to be a major cause of degradation of Banj oak (Singh et al., 2016). A vegetation study conducted by Gairola et al. (2010) in the Mandal valley had found Banj oak *Quercus leucotrichophora* to be the dominant tree species at altitudes between 1500 to 1800 masl while this species, in general, contributed significantly to the climax plant communities of the Western Himalayas (Singh and Singh, 1992; Awasthi et al., 2003). Persistent cutting down of a forest's dominant species ultimately causes canopy gaps and reduced leaf fall, which, in turn, negatively affects the return of nitrogen to the soil. This changes ecosystem dynamics and consequently leads to poor regeneration across the forest (Yadav and Gupta, 2006).

In the Mandal valley, Banj oak branches are typically removed during winter for livestock fodder and for fuel (Singh and Rawat, 2012). An earlier study of the CHL in the Mandal valley also found that oak was one of the most important food in the winter diet of the species (Nautiyal, 2015). This investigation also showed Banj oak trees, especially at high-density sites, to be chosen more over other tree species as food and also as sleeping trees. The high dependency of the villagers on this oak was, therefore, likely to be the primary factor leading to the reduction of dense oak patches within langur home ranges, thus driving them to raid agricultural fields for food, causing high levels of crop damage. Moreover, the langurs were unable to utilize all parts of their home range equally because of the loss of high-density oak patches. This, in turn, seemed to make them frequently re-use some sites more than others,

leading to overcrowding at the sleeping sites and a further reduction of their food resources near these sites.

3.5.2. Can Quercus replanting promote peaceful coexistence between human and langurs?

At the current rate of global agricultural land expansion, agro-economic models predict a significant reduction of wildlife habitats by 2050, with farmlands occupying an additional 200–300 million hectares across the world (Schmitz et al., 2014). Habitat loss due to anthropogenic activities is a key factor driving the decline in the number and habitats of many wildlife species in their native habitats. It now seems evident that the affected species can perhaps only be conserved by devising strategies for peaceful coexistence of humans and wildlife (Woodroffe et al., 2005), mainly by stemming habitat loss and minimizing negative human-animal interactions. One of the important steps in this direction would be to improve traditional techniques as well as develop new control methods to prevent crop-foraging by primates (Strum, 1994). Understanding the foraging and ranging ecology of the target nonhuman species is an obvious first step for the development of such mitigation strategies (Hill, 2005). Our study thus proposes a model incorporating the behavioral ecology of the target species and certain socioeconomic variables to address the suitable mitigation of crop-foraging by the study langur population. We recommend a long-term solution: the active conservation of *Quercus* forests and regeneration of high-density patches of the species, which serve not only as a critical food source for langurs during the harsh Himalayan winter (Nautiyal, 2015) but is also necessary to provide them with shelter and protection from potential predators. This model, we believe, may be applicable to a wide variety of wildlife species residing in forest-agricultural ecotones, not just in the Himalayan ranges but in other landscapes as well. Animal crop-foraging, especially by primates, is often directly correlated to key food resource availability in forest habitats (Strum, 1994; Treves et al., 1998; Siex et al., 1999; Tweheyo et al., 2007; Hockings et al., 2009) and hence, a detailed understanding of the key food plant species in decline and the role of these species in the diet of the target wildlife species should be a priority in formulating conflict mitigation strategies.

Quercus species have been widely reported as important food sources for Himalayan langurs residing in marginal habitats across their distribution range. One of the pioneering studies conducted in the Indian Himalaya by Sugiyama (1976), for example, showed that *Q. incana* fruits were the most important food resource for langurs in all six months of the study.

Furthermore, for langurs inhabiting alpine meadows, where food resources are scarce throughout the year and negligible in winter, their main food, before the onset of harsh winter, was *Q. semecarpifolia* (Nautiyal and Huffman, 2018). Minhas et al. (2010) suggested that *Q. incana* was one of the essential species used both as sleeping trees and as an important food resource in both summer and winter by langurs in the Hindu Kush Himalayan range. Similarly, Bishop (1975) noted that in the Nepal Himalaya, *Q. semicarpifolia* was often used as sleeping trees and as an important food source for the local langur populations.

3.5.3. Future goals for coexisting with langurs

Based on the results of this study, we have already identified and begun to implement three short- and long-term activities to help mitigate human-langur conflict in the Mandal valley; these activities are also likely to be applicable to other similarly affected areas in other *Quercus*-dominated regions. (1) Replanting efforts: As the degradation of the local forests, oak trees in particular, through human activities seems to have resulted in a decrease of available food and shelter resources for langurs, in turn leading to the observed recent increase in crop-foraging at our study sites, we have initiated the restoration of the degraded oak forest through planting of *Quercus* in the forests surrounding the study villages and intensifying the planting of alternative fodder trees other than oak. We hope that this would help reduce langur visitation rates at the villages and their raiding of the adjacent crop fields. (2) Environmental education outreach: Environmental-awareness outreach towards young children is a rather important strategy for forest protection. as they are the future decision-makers and can potentially influence the behavior of their parents now by discussing with them what they have learnt at school. We have begun outreach programs in government primary schools in each village by engaging them in different competitive activities to enhance their interest toward nature. Taking children into the forest also offers them first-hand experience with wildlife that they might not have otherwise been exposed to, free of the cultural interpretations of the value of wildlife from the perspective of adults, who often see wildlife as a threat, not as a source of knowledge. (3) Empowerment of women in the community: Nearly 95% of all agricultural work, the collection of fodder and of firewood is done by women. In spite of their central role as caregivers and providers, they receive very little return for their efforts other than producing the resources that the family needs to subsist on. Providing basic education and the means of obtaining alternative incomes empowers women, providing them with alternative choices and means to sustainably utilize forest resources, and this, in turn, indirectly promotes the conservation of wildlife and

natural resources.

Our study thus establishes that crop damage by wildlife is often brought about in part by the human activities that the local communities indulge in to maintain their precarious livelihoods and to enhance their economic base. They obviously cannot be blamed for this but it is, nevertheless, important to increase conservation efforts to protect the local environment and the wildlife that it supports, while also improving the daily lives of the farmers. These two endeavors need to be strongly interconnected, as is clearly evident from our explorations on this high-altitude farming community, as indeed may be the situation for many others across the greater Himalayan region of the Indian subcontinent.

Conclusions

Our study is possibly the first ever on crop-foraging by a Himalayan langur species, with important implications for other Himalayan zones. Our questionnaire surveys clearly revealed the ecological importance of Banj oak in habitats where socioeconomic conditions and low agricultural production appeared to be the main reasons for over-exploitation of forest resources for use as animal fodder. This was clearly perceived by the respondents to have led to an increase of conflict in the form of crop-foraging by langurs. Our findings also show Banj oak tree, especially at high-density sites, to be chosen more over other trees as food and also sleeping site. The high dependency of the villagers on this oak is, therefore, likely to be the primary factor leading to the reduction of dense oak patches within langur home ranges, driving them to raid agricultural fields for food and causing high levels of crop damage. Based on our results, we propose here a resource management strategy for mitigating human-langur conflict and promoting their coexistence, which could be applied to habitats dominated by *Quercus* spp. and where langurs and humans are both highly dependent upon this resource for survival. This model, we believe, may be applicable to a wide variety of wildlife species residing in forest-agricultural ecotones, not just in the Himalayan ranges but in other landscapes as well.

Table 3.1. Model characteristics

Models	K	AICc	ΔAICc	Weight	Cum.weight	Log-likelihood
crop-foraging by langurs						
Integrated	7	188.56	0.00	0.55	0.55	-87.01
Land-Pro-Live	6	188.96	0.40	0.45	1.00	-88.28
Inc-Pro-Live	6	202.94	14.38	0.00	1.00	-95.27
Pro-Live	5	203.01	14.45	0.00	1.00	-96.36
Live	4	213.27	24.71	0.00	1.00	-102.54
Income-Land-Pro	6	216.43	27.87	0.00	1.00	-102.01
Land-Pro	5	218.57	30.01	0.00	1.00	-104.14
Income-Pro	5	238.68	50.13	0.00	1.00	-114.20
Resource loss in village forests						
Land-Pro-Live	6	265.53	0.00	0.29	0.29	-126.56
Pro-Live	5	265.54	0.02	0.29	0.59	-127.63
Live	4	266.85	1.32	0.15	0.74	-129.33
Income-Pro-Live	6	267.58	2.05	0.11	0.84	-127.59
Integrated	7	267.62	2.10	0.10	0.95	-126.54
Land-Pro	5	270.05	4.52	0.03	0.98	-129.88
Pro	4	272.01	6.49	0.01	0.99	-131.91
Income-Land-Pro	6	272.15	6.62	0.01	1.00	-129.87

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Aikaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; K: Number of variables included; Land: Landholdings (ha); Live: Total number of livestock; Pro: Crop Production (Kg); Weight: Model probabilities.

Table 3.2. Variation in the household demographic and socioeconomic variables among five villages in the study area (N = 215 households).

Village	Total number of households	Total population	Percentage educated population	Total livestock population	Average/household		
					Annual production (kg)	Total agriculture land holdings (ha)	Total annual income (INR)
Gondy	33	155	92	98	319	5.0	179939
Khalla	53	261	91	152	539	10.8	177500
Kunkuli	23	117	87	105	244	6.1	181043
Mandal	33	171	93	92	448	8.3	210879
Siroli	73	351	90	375	249	3.5	186895

Table 3.3. GLMM analysis of crop-foraging by langurs and resource loss in the village forests in the study area.

Best model (Likelihood of crop-foraging by langurs)				
			AIC	***df***
			188	210
Fixed factors	**Estimate**	**SE**	**z value**	**p value**
Income	0.637	0.405	1.577	0.1150
Landholdings (ha)	-2. 248	0.612	-3.676	**0.0003**
Crop production (Kg)	-2.105	0.718	-2.105	**0.0034**
Total number of livestock	4.125	0.853	4.842	**1.29e-06**
Best model (likelihood of resource loss in village forests)				
			AIC	***df***
			265	210
Fixed factors	**Estimate**	**SE**	**z value**	**p value**
Landholdings (ha)	-0.620	0.433	-1.442	0.1494
Crop production (Kg)	-0.867	0.572	-1.517	0.1293
Total number of livestock	1.451	0.574	2.529	**0.0114**

Table 3.4. Model characteristics

Models	K	AICc	ΔAICc	Weight	Cum. weight	Log-likelihood
Sleeping site re-use by langurs						
Quadratic	4	74.30	0.00	0.66	0.66	-29.15
Cubic	5	75.65	1.34	0.34	1.00	-25.32
Degree-4 polynomial	6	85.80	11.50	0.00	1.00	-22.90
Degree-5 polynomial	7	113.24	38.93	0.00	1.00	-21.62
Feeding site re-use by langurs						
Quadratic	4	75.79	0.00	0.98	0.98	-29.90
Cubic	5	83.81	8.02	0.02	1.00	-29.41
Degree-4 polynomial	6	98.12	22.33	0.00	1.00	-29.06
Degree-5 polynomial	7	127.68	51.68	0.00	1.00	-29.74

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Aikaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; K: Number of variables included; Weight: Model probabilities.

Photo Plate 1. Crop-foraging by Group S in the Mandal valley, including feeding on (a) mustard plants, and (b) on wheat. (c) Village and agricultural land in the Mandal valley landscape, and (d) oak forests on the hillsides.

Photo Plate 2. Habitat use by Troop S in the Mandal valley, including (a) feeding on Banj oak acorns at the edge of Siroli village, and (b) using Banj oak as a sleeping tree. Dependency of the Mandal valley villagers on Banj oak, showing collection of oak leaves for (c) making cattle beds, and (d) cattle fodder.

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CHAPTER 4

INTERSPECIFIC FEEDING ASSOCIATION BETWEEN CENTRAL HIMALAYAN LANGURS (*Semnopithecus schistaceus*) AND HIMALAYAN BLACK BEARS (*Ursus thibetanus*), IN A TEMPERATE FOREST OF THE WESTERN INDIAN HIMALAYAS

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Chapter 4

Interspecific feeding association between Central Himalayan langurs (*Semnopithecus schistaceus*) and Himalayan Black bears (*Ursus thibetanus*), in a temperate forest of the Western Indian Himalayas

4.1. Abstract

One aspect of interspecific feeding associations is gleaning, or the acquisition of food resources by one species eating items that incidentally drop to the ground by another species while feeding. Gleaning is a widespread phenomenon between primates and ungulates, but such primate - carnivore gleaning associations are extremely rare in the literature. While studying the behavior and ecology of the Central Himalayan langur (*Semnopithecus schistaceus*) in the alpine zone (3300 m - 3500 m a.s.l.) of Rudranath, Kedarnath Wildlife Sanctuary, Uttarakhand State, India, we observed three direct instances and gathered indirect putative evidence of gleaning by Himalayan black bear (*Ursus thibetanus*) beneath large *Quercus semecarpifolia* trees with langurs feeding on acorns during the peak fruiting season. This is the first report of such a feeding association between langurs and bears, and the second for primates and carnivores.

4.2. Introduction

Interspecific feeding associations (IFAs) range from closely related species to species from different orders, and occur across a wide range of taxa (Stensland et al., 2003). Most of the documented relationships are mutualistic by nature, e.g. facilitating predator avoidance (Rasa, 1983; Landeau and Terborgh, 1986; FitzGibbon, 1990; Dickman, 1992; Makenbach et al., 2013) or promoting higher foraging efficiency (Cody, 1971; Székely et al., 1989; Oommen and Shanker, 2010).

One type of IFA is gleaning, the acquisition of food resources by one species picking up and eating items that incidentally drop to the ground by another species while feeding (Newton, 1989). Gleaning associations involving primates are abundant in the literature. To date, at least 174 different examples involving 64 primate species (20 genera, seven families) and 95 non-primate species (73 genera, 35 families) have been documented (see Heymann and Hsia, 2014). Primate–ungulate gleaning associations, including bovids and cervids, are most common across both Africa and Asia (e.g. Morgan-Davies, 1960; Elder and Elder, 1970; Hill, 1974;

Whitten et al., 1988; Newton, 1989; Tsuji et al., 2007, 2015, Ramesh et al., 2012), with only one report from the Neotropics (Agoramoorthy, 1997). Apart from this, there are reports of birds, reptiles, and fish (e.g. Glander, 1979; González Kirchner, 1996, Sabino and Sazima, 1999) gleaning foods dropped by primates.

Gleaning shows a strong asymmetry in the type and distribution of benefits with the main benefactors usually being the animals that gain access to food incidentally dropped by foraging primates. There is only one case of gleaning reported between a carnivore, the golden jackal (*Canis aureus*) and a primate, the Hanuman langur (*S. entellus*), in the lower altitudes of central India (Newton, 1985). The fruits of *Ficus infectoria*, *Syzygium cumini* and *Buchanania lanzan* were incidentally dropped by langurs and gleaned by golden jackals from the ground. Although jackals may prey on young langurs, they are not a threat to langurs in the trees.

Here, I describe three instances of gleaning between high altitude living Central Himalayan langur (*Semnopithecus schistaceus*) and Himalayan black bear (*U. thibetanus,* Carnivora*)*. Himalayan black bears are known to eat langurs and even livestock when their preferred vegetable matter foods are scarce (Bishop, 1975; Sangay and Vernes, 2008), making this a particularly unique association. To the best of our knowledge, this is the first report of gleaning between primates and bears.

4.3. Materials and methods

This research was conducted in Rudranath (30.5°N, 79.3°E; 3400 m – 3800 m a.s.l.) located in the Kedarnath Wildlife Sanctuary (KWS), one of the largest designated Protected Areas in the Chamoli-Rudraprayag district of Uttarakhand, India. KWS covers an area of 975 km^2 (Figure 4.1). The study area was a high altitude alpine area, consisting of two forest types: sub-alpine scattered tree and scrub (2800 m – 3400 m a.s.l.) and alpine meadows and rocks (> 3400 m a.s.l.; Champion and Seth, 1968). The dominant tree species is oak, *Q. semecarpifolia* found in the sub-alpine area.

The year in the study area is divided into three main seasons; a cool and relatively dry winter (November to March); a warm and dry summer (April to June); and a warm and rainy monsoon period (July to September) with transitional periods of February to March (Spring) connecting winter and summer, and October to November (Autumn) connecting the rainy and winter

seasons (Gairola et al., 2010). The mean maximum temperature between April and November in Rudranath is 15.1°C, with a minimum temperature of 1.0°C. Mean relative humidity ranges from 43% to 98% (Bisht et al. 2014). The snow melts during April-May, producing an abundance of soil moisture. The climate is harsh with low temperatures, fluctuating atmospheric pressure, blizzards and hailstorms prevailing most months of the year. Even in May, well before the beginning of the monsoon, cloud and fog formation is common. In winter, snowfall is heavy covering most of the study area (Billings, 1973).

Figure 4.1. The Kedarnath Wildlife Sanctuary in Chamoli-Rudraprayag district, Uttarakhand, India. The study area is indicated with a building icon in the map which represents a Hindu temple.

Our observations were made between June and September 2016. The campsite was 7 km from the survey area, and we walked to the area daily along a fixed trail. The observations were carried out by four people on any given day, searching for, following, and habituating one troop of langurs, from morning (6 a.m.) to evening (6 p.m.), independent of weather conditions. As part of this daily routine, we systematically collected any indirect evidences of bears and their activity, i.e. scat, feeding traces, scratch marks on trees, sleeping dens, and footprints. Behavioural observations were carried out by naked eye or through binoculars (Olympus 8×40) for general activity (feed, travel, rest, play, social interactions, and others) by 15-minute scan

sampling at five-minute intervals (Altmann, 1974). Activity for each visible individual was recorded at the moment it was first observed. For individuals that were feeding during the scan, we recorded food species and plant part eaten.

The langur study group contained five adult males, seven adult females, eight sub-adults, and six juveniles. We spent a total of 468 hours (h) looking for and following langurs and looking for signs of bear activity, and an approximately equal number of hours were spent each month; June (109 h), July (118 h), August (127 h) and September (113 h). All direct sightings of both species were recorded.

4.4. Results

4.4.1. Langur feeding behavior

Langurs were observed to spend the majority of their time feeding on *Q. semecarpifolia*, until the acorns were almost totally finished at the end of September. Langurs spent the rest of the time feeding on young leaves of *Betula utilis* and *Sorbus microphylla*. Time spent feeding on acorns was highest in July (61%) and lowest in September (6%, Table 4.1). In September, the langurs split up into two groups. Only one of these sub-groups could be found in the area, and they continued feeding on the remaining acorns.

4.4.2. Direct evidences of bear gleaning

We encountered one adult female bear twice and sub-adults three times (Figure 4.2) in the month of July and August. Gleaning by bears was observed only in July and August (Table 4.1), the peak period for langur acorn consumption. Three times we directly encountered bears gleaning acorns of *Q. semecarpifolia* on the ground that were incidentally dropped by langurs feeding above in the tree. Coinciding with peaks in langur feeding on acorns, our indirect evidence of Himalayan black bears in the study area also increased in July and August (Table 4.1).

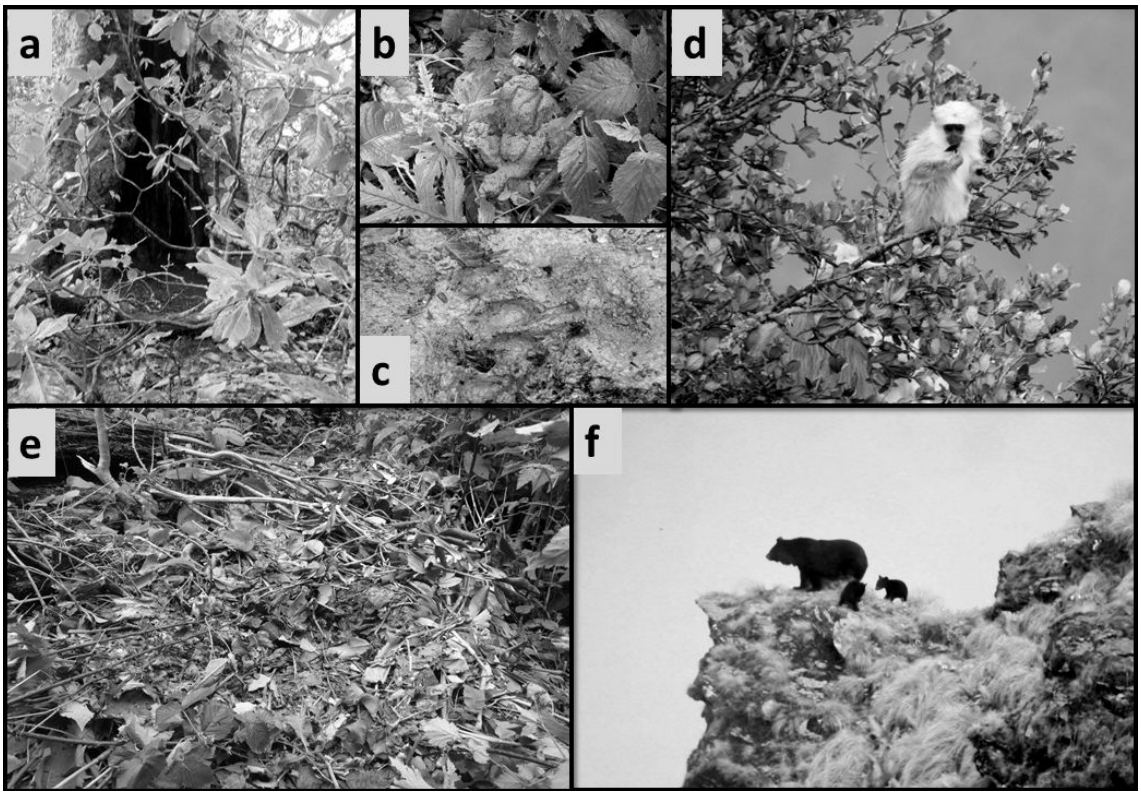

Figure 4.2. Photographs suggesting the possible langur-bear association. a: bear den, dug out of a hollow standing tree; b: bear scat; c: bear footprints; d: a juvenile of the Central Himalayan langur feeding on *Quercus semecarpifolia* acorns; e: ground nest made by bear, f: an adult female with her cubs of the Himalayan black bear.

4.4.3. Indirect evidence of langur-bear association

We frequently found bear scat (Figure 4.2) under acorn trees where langurs had recently been observed feeding. The scat consisted mostly of digested acorn matter, as indicated by the pale, soft fecal matrix (Figure 4.2).

Bear scat deposition and ground vegetation destruction, apparently, the result of searching for food, were frequently found in the langurs' home range area (Figure 4.2). Additionally, indirect evidence of bear activity in the langur home range were four daily sleeping dens, dug out of hollow standing trees and one ground nest with fresh feces deposited nearby (Figure 4.2). Partly attached broken branches up in a tree, a sign of bear feeding, were never observed, unlike what we commonly found at lower elevations, 1500 m to 2500 m a.s.l. (Nautiyal, personal observation).

4.5. Discussion

4.5.1. The nature of langur-bear gleaning interactions

The langur-bear feeding association described here appears to be beneficial for the bear to gain access to fallen *Q. semecarpifolia* acorns. What makes this association perhaps unique from other reports involving primates however is the fact that Himalayan black bears are potential predators of langurs, and have been reported to kill langurs in neighboring Nepal (Bishop, 1975). While more observations are needed to make firm conclusions about the benefits and detriments of this association for langurs, we think that the nutritional benefits of gleaning highly nutritious acorns by bears outweighs the risk and energy expenditure of hunting, especially for females with their cubs (see below), at this critical time of year in Rudranath.

The black bear is normally omnivorous, but when food is scarce they are known to sometimes hunt. In the situation we report here however, the relationship was about getting seasonally available acorns fallen to the ground, a favored high energy content food item (McDonald and Fuller, 2015). *Quercus semecarpifolia* is the dominant tree of the sub-alpine and alpine forest between 2100 m and 3800 m a.s.l. (Singh and Singh, 1992) and flowering time is typically in June and July, with August being the peak fruiting period (Shrestha, 2003). Bears select or shift habitats based not only on the distribution of food-producing plants, but also on the phenological development of these food plants (Davis et al., 2006; Koike, 2009). During our study, langurs and bears were found together during the short *Q. semecarpifolia* fruiting season (July and August). As mentioned, the IFA described here involving females and their cubs occurred in the month of July and August, which is right before winter. For such bears acorns may be an important nutritional source for accumulating fat in preparation for the harsh winter ahead (Garshelis and Steinmetz, 2008).

In this situation, it seems necessary for bears to minimize their expenditure of energy for foraging or hunting to maximize energy and fat stores. If so, then we would expect them to prefer the most easily available rich resources for themselves and their cubs. Hunting agile prey like langurs up in the canopy is not itself an easy task which involves climbing up in these tree, balancing on the thin branches to capture a langur. Thus, considering energy management, bears should prefer to glean the acorns rather than attempting to go after langurs high up in the oak canopy at Rudranath.

4.5.2. Why glean instead of forage in the trees?

Why did not we see bears climb up into the trees to forage on acorns themselves instead of gleaning them from the ground under langur feeding trees? Based on the observations reported here, we present three possible non-exclusive hypotheses to help explain this.

1. Increased foraging efficiency: In the alpine meadows of Rudranath, food resources are scarce throughout the year and negligible in the winter. *Q. semecarpifolia* is the dominant tree in the study area. During our study, langurs and bears were found together during the short *Q. semecarpifolia* fruiting season (July and August). We noticed that the common feeding patches used by langurs and bears had higher concentration of fruiting *Q. semecarpifolia* trees as compared to other patches in the study area. In principle, bears can climb up trees to get acorns but the energetic cost involved in finding fruiting trees, climbing up into them and taking acorns from the terminal branches where they are found seems much greater, compared to simply gleaning them from forest floor. Following a langur troop and gleaning acorns on the ground, may help bears, especially females with young cubs (see below), to easily locate fruiting trees in the forest, increase foraging success, and reduce energy expenditure. This strategy adopted by bears could help them to more effectively store energy needed to prepare themselves, and their cubs, for the upcoming harsh winter.

2. Offspring protection: Infanticide is a widespread behaviour by adult male bears and coincides with the breeding season of Asiatic black bears from mid-June to mid-August (our study period) (e.g. LeCount, 1987; Bellemain et al., 2006; Libal et al., 2011; Steyaert et al., 2013) It is reported that during each breeding season, several males compete for breeding privileges with females. The langur-bear IFA described here coincided with this period of high risk of infanticide. For females with cubs, it is probably a safer option to follow langurs and glean the acorns from the forest floor, instead of leaving their cubs vulnerable to possible infanticide by males on the ground. At this stage, the cubs are too big to cling to mother but too small to climb up large girthed, tall trees.

3. Risk of Falling: At our site, timberline *Q. semecarpifolia* are conspicuously wider girthed and taller (average 225 cm diameter, 15 m height, n = 60) than at the lower elevation *Q.*

leucotrichophora (1500 m – 2500 m a.s.l.) in our study areas (average 87 cm diameter, 10 m height, n = 40). Bears are generally good climbers, but adults become too heavy to climb out onto to the terminal branches where acorns are found. The risk of falling for a bear seems to be considerably higher in these taller trees, especially on terminal branches while reaching out for acorns. At the lower elevation site, bears frequently foraged and even built daily tree sleeping nests up in the shorter and smaller girthed *Q. leucotrichophora* trees, but this was simply never seen at Rudranath during our study (Nautiyal, personal observation).

We propose that this IFA is not a chance encounter, but rather an adaptive bear survival strategy, perhaps for females in particular, to combat lean times when access to highly nutritious food resources are scarce in high alpine meadows of the Himalayas.

Table 4.1. Feeding activity of Central Himalayan langur and Himalayan black bear activity between 3300 m-3500 m a.s.l. at Rudranath.

Month	**June**	**July**	**August**	**September**
% individuals feeding on acorns by langur (total number of feeding records in scan samples / month)	10.3 (58)	61 (359)	39.3 (351)	6 (200)
Direct bear sightings	0	2	3	0
Direct sightings of bear gleaning oak fruits under the langur feeding tree	0	2	1	0
Fresh bear scats encountered	1	25	32	6
Fresh tree scratch marks encountered	0	8	6	2
Fresh pugmark encountered	1	10	12	3

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CHAPTER 5

ANTI-PREDATOR STRATEGIES OF CENTRAL HIMALAYAN LANGURS (*Semnopithecus schistaceus*) IN A HUMAN DOMINATED LANDSCAPE

Photo credits: Himani Nautiyal

Chapter 5

Anti-predator strategies of Central Himalayan Langurs (*Semnopithecus schistaceus*) in a human dominated landscape

5.1. Abstract

The evolution of predator-prey relationships is an important topic in primatology, and many aspects of primate society have been explained as a response to predation pressure. While predation has been discussed in broad theoretical terms, few systematically collected data exists on the subject. To address this gap in knowledge, predatory dog-primate interactions were studied in a 78 member group of habituated, individually recognized Central Himalayan langurs (CHL) (*Semnopithecus schistaceus*) living in a high-altitude subsistence agricultural landscape of northern India. I recorded 312 langur-dog interactions over two years. Predation by dogs occurred most often when langurs approached the open agricultural fields from the forest. These predation events resulted in 15 lethal attacks, in 8 of which the prey was consumed. In response to dog predation, males performed three types of anti-predator behaviors; direct fighting with a predator, giving alarm calls, and fleeing or freezing response. Long-term resident adult males engaged in most of the direct fighting with dogs, and were responsible for rescuing females and their infants from attacks. Less experienced immigrant and high ranking males tended to perform the less risky behaviors more frequently. Results show that the likelihood of engaging in high-risk anti-predator behavior by CHL adult males is better predicted by the residency duration, genetic relatedness, grooming rate and social rank. It is proposed that accumulated knowledge about predatory dog behavior by the long-term resident males is favorable for engaging in high-risk encounters with predators. This type of behavior might be related to the males' enhanced social bonds with females. Moreover, males who are related to the females fought more with dogs than non-kin.

5.2. Introduction

Predation is a major evolutionary force that has resulted in a variety of adaptations to avoid and deal with predators (Lima and Dill, 1990; Caro, 2005). Interactions between predator and prey are regarded as an evolutionary "arms race" that occurs over a historical time scale (Dawkins and Krebs, 1979). Predation in primates is also considered to be an important factor

responsible for the evolution of primate societies (Cheney and Wrangham, 1987). Indeed primates seem to have many predators: in one review, 174 predators species were recognized, including carnivores (small and large), raptors, canids, hyaenids and reptiles (Hart, 2007). However, most previous studies on primate predator-prey interactions are lacking in great detail, because systematic observations of such rare events are difficult in the wild (Stanford, 2002). Recently some creatively designed experimental approaches have contributed to the growing understanding of such interactions (Miller and Treves, 2012).

Anti-predation strategies are widespread among animal taxa, and act largely to diminish the risk of being detected or captured by a predator. One strategy is to give alarm calls in the presence of predators; these warn nearby conspecifics about potential threat, and occur in almost all primate species (Cheney and Wrangham, 1987; *Curio,* 1978; Zuberbühler et al., 1999). Some primate species are known to confront predators directely, by what is known as 'mobbing' or 'counterattacking' (Crofoot, 2012; Tórrez et al., 2012). Such aggressive defense against predators is observed in multi-male primate societies, such as yellow baboons (*Papio cynocephalus*), where males have been observed to kill domestic dogs (Stoltz and Saayman, 1970). An adult male capuchin monkeys (*Cebus capucinus*) was reported to hit a venomous snake with a sticks (Boinski, 1988). As freezing or fleeing may a less costly anti-predation response, individuals performing higher-cost behaviors (alarm calling or counterattacking) should gain some fitness benefit from these actions (Curio and Regelmann, 2010). Dugatkin and Godin (1992) suggested six major types of cost: increased risk of mortality to self, increased risk of mortality to relatives, lost mating opportunities, lost feeding opportunities, energetic costs of approaching a predator, and costs of being exploited by others. For instance, a yellow baboon was once observed being killed by a leopard it had attempted to mob (Cowlishaw, 1994). Similarly, a jaguar was once observed to kill a mobbing capuchin monkey (Tórrez et al., 2012). Although the risk of being killed by a predator during a counterattack may be relatively low, the cost is absolute. Consequently, energetic costs of performing alarm calls and counterattacks may be minor but they are paid regularly (Crofoot, 2012).

Why do primates take such risks in the first place? There are several hypotheses regarding the benefits to males of performing such high-cost behaviors. The '*predator-prey interaction'* hypothesis posits that prey will approach a potential predator to obtain information about intent to attack, and modify its behavior according to the level of risk and the proportion of cost to benefit of further interacting with the predator (Dugatkin and Godin, 1992; Maklakov, 2002).

Predators are not always motivated to feed on potential prey species, therefore by approaching a predator an individual can assess its motivation, and then take appropriate anti-predator measures (Helfman, 1989).

The '*reciprocal altruism*' hypothesis suggests that an individual may perform costly act that benefits another, unrelated individual, and will be repaid in the future (Trivers, 1971). It was subsequently proposed that the cumulative cost and benefit of an altruistic act, as it benefits the recipient, surpasses the cost to the altruist, so that the future cumulative benefit for both individuals will exceed the cumulative cost of their altruism. Therefore, natural selection would favor those individuals who are more likely to reciprocate at a later time (Packer, 1977). For instance, adult olive baboon (*P. anubis*) males form coalitions against a single opponent to secure access to sexually receptive females. Moreover, males were more likely to join future coalitions with males who helped them previously (Packer, 1977). However, many examples of altruistic behavior in the literature are debatable, due to low cost to the actor (Clutton-Brock, 2002; Schino, 2007). High-cost behavior such as direct encounters with a predator might provide a clearer picture with regard to this hypothesis.

The '*costly signaling*' hypothesis posits that individuals self-advertise high-quality traits through the ability to stay in the vicinity of a predator to indicate their quality as a mate or their willingness to cooperate with others (Zahavi, 1975; Zahavi, 1995; Dugatkin and Godin, 1992; Maklakov, 2002). Individuals who exhibit costly signals honestly advertise their quality or condition, as only healthy and fit individuals are able to do this (Grafen, 1990; Vega-Redondo and Hasson, 1993). Consequently, if anti-predator behavior signals one's high quality as a mate, high-quality individuals will be more likely to achieve more reproductive success (Arnold, 2000). For example white-throated magpie-jays (*Calocitta formosa*) use predator interactions to advertise their presence and availability as a potential mate (Ellis, 2009).

The '*kin selection hypothesis'* posits that animals help others with whom they share genes by common decent, promoting the spread of those genes within the population (Hamilton, 1964). Kin selection has been especially illustrated and explained using social insect models (Queller and Strassmann, 1998). In primates, the role of kin selection has been studied especially with regards to common behaviors such as social grooming and coalition formation, it has been considerably less studied in relation to anti-predatory responses (Silk, 2002). The function of alarm calls in belding's ground squirrels (*Spermophilus beldingi*) is to alert relatives about

imminent danger, as they alarm call more frequently when relatives are nearby (Sherman, 1977). Similarly, chipmunk (*Eutamias sonamae*) alarm call frequency is correlated with the probability that kin are within auditory range (Dunford, 1977).

The above-mentioned hypotheses have been tested in a variety of different taxa (Dugatkin and Godin, 1992; Maklakov, 2002), but primates remain under-represented in this literature (Stanford, 2002). Globally, free-ranging dogs are well known for predating on native wildlife (Ritchie et al., 2013; Doherty et al., 2017). Dog predation on primates is mostly reported from areas where primate species live in close proximity to humans, e.g. macaques and langurs in Asia (Anderson, 1986; Riley et al., 2015; Najmuddin et al., 2019) and gelada baboons (*Theropithecus gelada*) in the open highland grasslands of Ethiopia (Iwamoto et al., 1996). India has one of the highest dog populations of any region in the world (Gompper, 2014). Moreover, online survey data in India revealed that 73% of respondents reported dog attacks on wildlife, and that 45% of those attacks resulted in death and consumption of the prey (Home et al., 2018). Langurs and domestic dogs frequently encounter each other in human dominated-landscapes (Nautiyal et al., 2020; Chapter 3). Primates living in such environments gain advantages through the use of their intelligence, agility, dexterity, and high levels of sociality and cooperation, combined with dietary and behavioral flexibility (Else, 1991). Therefore, primate populations living in such environments should show behavioral flexibility for coping with the serious threat from predatory dogs. I took advantage of this situation at my study site to better understand primate anti-predator behavior and the possible costs and benefits incurred by the Central Himalayan langur (*Semnopithecus schistaceus*) (CHL), whose home range overlaps with agricultural fields, a seasonally important food resource for them (Nautiyal, 2015).

CHL are seasonal breeders and reside in multi-male multi-female groups. Females are philopatric, while males disperse from their natal group at a mean age of 6 years (before reaching adulthood) and enter all-male groups (Sugiyama, 1976; Perlman et al., 2016). Secondary dispersal happens when males leave these all-male groups and immigrate into a multi-male multi-female group nearby or farther away, or else they re-integrate into their natal group (Borries, 2000). Adult males immigrate into a new group primarily during the mating season, which is from early June until late December (Sugiyama, 1976). CHL males are larger than females, and they play an important role in predator defense, including the emitting of loud vocalizations such as alarm calls (Bishop, 1979).

To elucidate the costs and benefits associated with langur anti-predator behavior, I investigated the relationships among the types of anti-predatory behavior displayed (high risk: counterattack, alarm calls; low risk: flee and freeze), adult male attributes (rank, residency duration, genetic relatedness to the group), and potential benefits (mating, grooming). Based on existing anti-predation hypotheses and information about langur behavioral ecology discussed above, I made the following five predictions: 1) High-ranking, newly immigrant males will perform more high-risk anti-predator behaviors. 2) Males sharing the same mtDNA haplotype with group females will perform more high-risk behaviors than males with no relatives in the group. 3) Longer-tenured males, having more exposure to village dogs, will perform more high-risk behaviors than males with shorter residency. 4) Males that exhibit high-risk behaviors will have strong grooming bonds with females. 5) Males that exhibit high-risk behaviors will have higher mating rates.

5.3. Methods and materials

5.3.1. Study site and population

Research was conducted on the S group in Mandal valley, Chamoli, Uttarakhand, Garhwal Himalayas, India (1500 - 1800 meters above sea level) from May 2017 to November 2018. HN established the research site in 2014, and fully habituated the group by June, 2016. All group members and newcomers were individually identified and monitored throughout the study period. In 2017 the group size was 71, and in 2018 it was 78 individuals (Table 5.1) (see Nautiyal 2005; Hasegawa et al., 2018; Nautiyal et al. 2020, for further details of the study site).

5.3.2. Behavioral Data collection

Data were collected on all 9 adult males when each was present in the group during the periods May 2017-November 2017 and June 2018-November 2018. Individual identification was done using physical characteristics such as body size, body shape, fur color and scars. HN also made a photographic catalog of all individuals to cross-check the identification between study periods and among field assistants. At any one time three observers (the author, HN and 2 assistants, PB and HM) were present at the study site. Inter-observer reliability of identification was assured by testing identifications using the photo catalogue. HN and one assistant collected

focal samples for male grooming and mating behavior. Agreement on focal sample events between the two observers was significantly different from chance (Cohen's kappa, HN-HM: k=0.72, p<0.001) (Cohen, 1960), with values between 0.60 and 0.74 considered good agreement (Watkins and Pacheco, 2000). The group was followed from 06:00 to 18:00 each day, on average for 25 days per month. Whenever dogs approached the langurs, a dog-langur encounter began, and one observer recorded all observed responses of each adult male present during the encounter *ad libitum* (Altmann, 1974), until the dogs left or where affectively chased away. I divided langur responses into three categories: 'alarm call', 'counterattack', and 'flee and freeze'. A male's response in any given encounter was usually consistent no matter how many responses were recorded. In only 3% (63/1908 responses) of cases, did males involved in an encounter give two different types of responses. Pseudo-replication was accounted for in the model described below. The behaviors of all visible males were recorded. Each predation event was recorded, noting the age and sex of the victim.

In total, 737 hours (mean 81.89 ±3.99 SE) of focal observations (15 minutes per session) of the 9 adult males were also recorded. For focal observations, adult males were chosen randomly and observations were balanced across time of day. From these data, male-female grooming and mating interactions were extracted. Male-male dyadic displacement interactions for rank analysis were collected from *ad-libitum* data (Altmann, 1974).

The study was conducted mostly during the mating season of in both years, when non-natal males were entering or leaving the group. Presence and absence of all males were recorded each day. The duration of group residency for each adult male was defined as the total number of days a male stayed in the group. Identification started in 2014 for all adult males in the group at any time, and the duration of residency was based on all attendance records collected between 2014 and 2018, during months when the group was being monitored.

5.3.3. Behavioral definitions

Alarm calls in Himalayan langurs (*S. ajax*) are defined as a multiple phase bark or bark threat call (Bishop, 1979). They are typically given when a potential predator is detected. I noted that males gave alarm barks only when dogs approached the group or chased a group member. In response to alarm calls, other individuals became alert, vocalized, or fled the area, stopping other activities that they were engaged in, such as grooming, mating, feeding or playing.

Counterattack is defined as the aggressive behavior directed at a dog (Crofoot, 2012), including aggressive slap, aggressive grunt, push, bite and pull.

Flee and freeze behavior is defined as escape from the ground to nearby high canopy when a dog approaches. Males already in the trees when a dog approaches tend to freeze and remain still. In this way they avert from any interactions with the dog.

Sexual behavior was based on descriptions given by Sommer et al. (1992). I categorized the following behaviors: 1- receptive behavior: copulation, sexual solicitatations resulting in a male mounting a female followed by pelvic thrusting, 2- female attractivity: male visual, tactile or olfactory inspection of a female's anogenital area, 3- proceptive behavior: Female sexual solicitation towards a male by head-shuddering, lowering of the tail, and presentation of the anogenital area without subsequent copulation.

Grooming is defined as the 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). The direction of grooming, giving or receiving, was noted.

5.3.4. Noninvasive sample (feces) collection, DNA extraction, PCR and DNA sequencing

To clarify whether each adult male originated from the study group or not, as well as the genetic structure of the study group, mitochondrial DNA (mtDNA) sequences were examined for a total of 54 individuals (69 % of all the members of the study group), including all adult males (see Appendix Table 5.1). Each individual was recognized by unique physical characteristics. Fecal samples were collected only when identity of the individual could be directly assigned to the sample. Using a cotton swab, epithelial cells of intestine were scoured off from the surface of feces and preserved in a lysis buffer [0.5% SDS, 100 mM EDTA (pH 8.0), 100 mM Tris-HCl (pH 8.0), and 10 mM NaCl] (White and Densmore, 1992). Since the amount of DNA obtained from feces was small, each individual was sampled multiple times.

DNA extraction was carried out from the lysate (fecal sample in lysis buffer) using a DNA cleanup system (Wizard SV Gel and PCR Clean-Up System, Promega, Madison, WI, USA), according to the method of Kawamoto et al. (2013) with slight modification. Before the first step of these procedures (Kawamoto et al., 2013), 1 mL lysate was incubated with 40 μL Proteinase K solution (20 mg/ mL) at 65 ˚C overnight. The 3 mitochondrial regions were examined to detect intraspecific variation in the Central Himalayan langurs: the control region (CR, so-called D-loop), cytochrome b gene (CYTB), the 1.8 kb region that spans the full length

of CTYB, tRNA-Thr, tRNA-Pro, and the 1st hypervariable segment (HVS1) of CR. Of the 54 individuals, 32 (11 adult females, 9 adult males and 3 subadult males) were selected for analysis of all 3 regions of mtDNA since it was expected that all the haplotypes of the study group would be detected from those individuals when considering the langurs' life history. Next, the remaining 22 individuals were examined for CR. Polymerase chain reaction (PCR) was performed to amplify each of the 3 mtDNA regions with a 40 μL reaction mixture [1.5 μL fecal DNA solution, 20.0 μL 2x PCR buffer, 8.0 μL 2mM dNTPs, 1.2 μL forward and reverse primers (10 μM), KOD FX (TOYOBO, Osaka, Japan) and 7.3 μL distilled water]. The thermal cycling condition for all 3 regions consisted of the initial denaturation at 94˚C for 2 min, 35 cycles of denaturation at 98 ˚C for 10 sec, annealing at 58 ˚C for 30 sec and extension at 68 ˚C for 1min, and a final extension at 68 ˚C for 5 min. I used the primers described by Khanal et al. (2018) in PCR of CR and CYTB. The primers for PCR of the 1.8 region were designed for this study: forward, 5'-TAATTCAACTACAAAAACAC-3', and reverse, 5'-TTTAAGGGGAACGTGTGGGCG-3'. After PCR, the PCR product was purified using the DNA cleanup system (Wizard SV Gel and PCR Clean-Up System, Promega, Madison, WI, USA). The purified DNA was used in a sequencing reaction with a BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). DNA sequencing was performed with the 3130 Genetic Analyzer (AppliedBiosystems). Sequence data for both directions were confirmed using the Sequence Navigator software (Applied Biosystems).

NUMT (nuclear copies of mitochondria sequences) is one of the problems in PCR and phylogenetic analyses using mtDNA sequence data (cf. Karanth et al., 2008). In the former, true mtDNA and pseudo mtDNA (from nuclear genome) sequences would be simultaneously amplified, and thus, results of DNA sequencing would not be successful due to overlapping of different DNA sequences. In the latter, results of phylogenetic analysis would produce unusual phylogenetic relationships. In most cases, a NUMT sequence is placed at a deviated position in the phylogenetic tree (Zhang and Hewitt, 1996). One of the reasons for this is that NUMT sequences evolve slower than true mtDNA sequences. To verify that the sequence data is from true mtDNA, we confirmed that CYTB sequences obtained here can be translated to amino acid, and that frame shifts and/or nonsense mutations do not occur in the amino acid sequence (Collura et al., 1996; Zhang and Hewitt, 1996). If the CYTB sequence in the 1.8 region was a true CYTB gene, the HVS1 region linked to the CYTB was also a true mtDNA sequence. Then, the HVS1 in the 1.8 region was compared to that of CR sequences. Because HVS1 is a part of CR, if the HVS1 is not a NUMT, the full sequence of CR is also not a NUMT. After this

procedure, sequence data were confirmed to be true mtDNA sequences. Translation of CYTB sequences to amino acids was carried out using GENETYX MAC ver. 16.00 (GENETYX, Tokyo Japan).

5.3.5. *Data analysis*

Residency duration was scored as the total number of days an adult male stayed in the group. I selected the starting point of the period of residency as when an adult male was first seen in S group. For those adult males present from the beginning of habitation in 2014, the first day of their residency period was set as June 3, 2014. Only two adult males remained in S group for the entire period of 2014 to 2018; the others appeared at different times during the study period. *Residency status* is divided into two types; resident and immigrant male. Adult males staying in the group for more than one mating season were called resident and those present for less than one mating season were classified as immigrant males. *Genetic relatedness* was assigned based on the mtDNA haplotype analysis described below.

Classification of mtDNA haplotypes (CR, CYTB and 1.8 kb for each individual of the langur) was performed using Sequence Navigator (Applied Biosystems) and GENETYX MAC software packages. All 3 data were successfully obtained from most of the adult females and adult males. All the mtDNA haplotypes detected in the study group were included in the dataset of adult females and adult males. Genetic structure of the study group was reconstructed using the CR data of 54 individuals (Appendix Table 5.1). Using GENETYX MAC, the CR sequences were aligned and the NEXUS data file was generated (1086 bp data set). After manually editing the NEXUS data file, cladistic analysis based on Templeton et al.'s (1992) algorithm was performed to estimate genealogical relationship among the individual CR sequences using TCS 1.21 software (Clement et al., 2000; 2002). The frequencies of mtDNA haplotypes in each age/sex class were also totalled. *Mating Rate* was calculated from the 749 observed copulations, recorded from the nine adult males across two mating seasons. Calculation for *Mating rate* was based on yearly total number of copulations for each adult male divided by the total number of days that the male was present in the group. *Grooming rate* was calculated using total number of hours of receiving grooming from females, for each male divided by total number of days male was present in the group. Dominance rank was determined using David's score (David, 1987) based on 3531 dyadic interactions and degree of linearity was determined using modified Landau's linearity index (h') (Vries, 1995). One

individual physically displacing another was considered as a dyadic displacement interaction (Hardy and Hardy, 1976). All dyadic interactions were converted to actor-receiver matrices for each year separately. The final rank was calculated using the mean David score over two years for each male (description of variables are presented in Table 5.2)

5.3.6. Model formulation and statistical analysis

To examine potential benefits of performing high risk anti-predator behavior, multinomial logistic regression (MLR) analysis was performed using *nnet package* (Venables and Ripley, 2002) in R, version 3.5.3 (R Core Team, 2019). MLR is used to model the nominal outcome variable, in which the log odds of the outcomes are modeled as a linear combination of the predictor variables. I categorized outcome variables based on the level of risk taken: high risk for alarm call and counterattack, low risk for flee and freeze. Low-risk behavior (flee and freeze) was the baseline for all the models tested, to get the effect of predictors on the probability of choosing high-risk behavior over low-risk behavior. Adult male identity was included as a random factor to control for pseudo-replication in all models. I determined five predictor variables to test the eight models (described above, Table 5.2). In R, I ran tests for homogeneity of residuals and variance inflation factors (VIF) below or around 1 (Field et al., 2012). To compare all models simultaneously, I used an information theory approach based on Akaike's information criterion (IT-AIC) to extract the best model to explain benefit of high-risk behavior by males during predator encounters (Burnham and Anderson, 2002). Such model selection criteria enable formal inference from more than one model (Johnson and Omland, 2004). The principle of this approach relies on ranking of the model from the candidate set of models using ΔAICc values ($\Delta i = AIC_{c(i)} - AIC_{c(min)}$) (Burnham and Anderson, 2002). Using the "aictab" function from the package *AICcmodavg*, I measured the model Akaike's weight, or relative likelihood, and accumulative weight of each model that indicates the extent to which one model is more likely than another in explaining the variance in the data (Mazerolle, 2016). The model characteristics are presented in Table 5.3. I used R package *steepness* for David score analysis (de Vries, 2014). I used the Spearman Rank Correlation to test for the correlation between male attributes.

5.4. Results

5.4.1. Dog predation on langurs

During the study period, a total of 312 dog-langur encounters and 1,971 langur responses during these encounters were observed. In these encounters, 12 village dogs were identified and classified into predatory (n=5) or non-predatory (n= 7), based on encounter history with langurs during the study. During these encounters a total 1,971 response of langurs, a total of 327 alarm call responses were directed towards dogs and conspecifics, 65% of responses were directed towards predatory dogs and 35% towards non-predatory dogs. Similarly, 155 counterattack responses towards dogs were observed, of which 75% were directed towards predatory dogs and 25% towards non-predatory dogs. Moreover, 1,489 flee and freeze responses, 53% were in response to predatory and 47% in response to non-predatory dogs. Overall, adult males showed significant differences in their behavioral response during these encounters depending on whether the dog had a history of being predatory or not (χ^2= 34.412; n=312; $p < 0.01$).

As consequences of the langur-dog encounters, 5 (7%) of the 71 group members were killed and 3 (4%) injured in 2017, while 3 (4%) of 78 group members were killed with another 4 (5%) injured in 2018 (Table 5.1). All successful predatory attacks by dogs took place in the agricultural field where langurs were exposed by the absence of connected tree cover, affording a low probability of escape. Sub-adults were the most likely to be killed, and these attacks took place in the agricultural fields because they tended to feed away from adult males, making it difficult for these males to immediately rescue them or chase the dogs away in time (Table 5.1). Although infants and juveniles were the most frequently injured age group by dogs, attacks led to no fatalities because adult males, adult females and their young offspring were always in close proximity when feeding in the agricultural fields. The adult males could quickly intervene either by directly attacking the dog or giving alarm calls. Dogs were more likely to attack infants in the forest (3 events), when they played away from mother. In the 7 observed langur kills by dogs, the victim was consumed right away (Figure 5.1).

The following examples describe instances of group males rescuing victims of dog aggression.

Observation 1, rescue of infant by adult males: 3 August 2018, between 9:50 and 10:05. Langurs are resting inside the forest in a big oak tree at the edge of an agricultural field. Two village dogs, Maya (adult female) and Bhuru (sub-adult male), are moving about in the area nearby the group. An infant (4 months old) is playing up in a small tree next to the big oak tree where all individuals are resting. At 9:50, the infant falls down and panics seeing the two dogs in front of him. He gives an alarm call. The dog Maya picks up the infant in its mouth and shakes it violently. Immediately, adult male langur Hari

rushes to the scene and starts fighting with the dog. Maya drops the infant from her mouth, but Bhuru pick him up and again shakes him violently. Many langurs now rush to the scene and start aggressively grunting at the dogs. At 9:52 Maya and Bhuru move about 5 meter away from the langurs; Bhuru continues shaking the infant in his mouth. Adult male langurs, Hari and Remo chase after the two dogs. Bhuru dropped the infant and it immediately picked up by the mother, who carries it back to the big oak tree. In appeared to us, it was almost impossible for the infant to survive, although it remained conscious and held onto its mother. Infant recovered and was observed alive throughout the remainder of the study. Hari and Remo chased both dogs away from the oak forest.

Observation 2, rescue of juvenile by adult males: 17 May 2017: Between 11:50 and 12: 16. At 11: 50 the langur group enters the agricultural fields located very close to Siroli village. At 11: 53 village dogs spot the group. At 11: 55, 3 dogs Sheru (adult male), Lalu (sub-adult male) and Kali (adult female) chase the group away from the agricultural field, isolating a juvenile male in a fig tree inside the fields in the process. The remaining group members move back to the cliffs adjoining the agricultural field. Due to the fragmented canopy cover, leaving the juvenile is effectively trapped in the small fig tree. All three dogs remain under the fig tree. At 11: 59, the juvenile emits loud alarm calls in the direction of the cliffs approximately 600 meters from the fig tree. 12: 06 two adult male langurs, Hari and Remo, leave the cliff and return to the tree where the juvenile remains trapped. Both adult male langurs produce loud alarm calls (louder than usual). At 12: 09, Remo runs toward the dogs and distracts them from the trapped juvenile, enticing the dogs to chase after him and engage in fighting. At 12:10, Hari approaches the lone dog remaining under the fig tree, still barking at the juvenile. Hari distracts the attention of this dog. At 12:12, both Hari and Remo scatter in different directions, with two dogs (Kali and Lalu) following Remo and one dog (Sheru) following Hari. All dogs are now more than 50 meters away from the fig tree and engaged in fighting with these two adult male langurs. At this time, the juvenile jumps to the ground and runs toward the direction of the cliffs and the rest of the group. At 12:16, the juvenile joins the group safely.

Figure 5.1. Dog-langur encounters. Sub-adult langurs were killed (a) and consumed (c) by dog. Adult male and dog fighting (b, d).

5.4.2. Adult male attributes

Nine adult males performed anti-predator behaviors; the details corresponding to each adult male are shown in Table 5.4. Adult male Batman was a temporary immigrant who stayed in the group only about 10 days, so he is excluded from all analyses. Adult males Hari and Remo were present in the group since 2014, therefore they had the longest period of residency. Other adult males entered the group during the start of the mating season between May and August of 2016, 2017 or 2018. CHL shows a linear dominance hierarchy (h'=1.00; n=9). Group residency was not correlated with rank (r=-0.416, p=0.2667, n=9). Some males entered the group and quickly became alpha (i.e. Julio, Viru and Thumri), whereas others came in at low-ranking positions (i.e. Muki and Orange). High-ranking males had greater access to receptive females and consequently higher copulation rates compared than lower-ranking males (r=0.859, p=0.0031, n=9), but they did not have a higher rate of grooming interactions (r=-0.189, p=0.6264, n=9) with adult females.

I found high genetic diversity among the adult males, represented by seven different mitochondrial DNA haplotypes (Appendix Table 5.2, Figure 5.2). Three males (Remo, Viru and Thumri) belonged to haplotype 1, 2 and 3, respectively, the only haplotypes associated with adult females in the group. It is likely that they left as immature males and returned as adults, similar to that described at Ramnagar. These males are maternal siblings of the study group. The remaining males had haplotypes not recognized in female group members, making these males true non-kin of group members (Table 5.4).

5.4.3. Factors responsible for antipredator behavior selection

Among eight models tested, the integrated model was clearly the best approximating model for explaining the benefit of anti-predator behavior. This model had the lowest AICc value and heights model probability (i.e., weight=1, Table 5.3), which include the variables *genetic relatedness, grooming rate, mating* and *residency duration.* The remaining seven models including the null model (Table 5.3) had a combined probability of less than 0.01.

The ratio of the probability of choosing to counterattack over fleeing and freezing by adult males with longer group residency was 0.002, whereas for choosing to give an alarm call was 0.001 (Table 5.5). Adult males with longer residency gave more alarm calls and directly fought with dogs significantly more compared to shorter residency males (Table 5.5; $z= 12.876$; $p<0.01$; $z=7.134$; $p<0.01$) (Figure 5.3d). The two longest-term resident males (Hari, Remo), performed counterattacks and alarm calls more than the rest of the adult males in the group (Table 5.4, Figure 5.4a and 4b).

Maternal siblings perform high rates of counterattack compared to non-kin males (Table 5.5; $z=2.085$; $p<0.05$). The ratio of the probability of counterattacking over fleeing and freezing by maternal sibling males was 0.393, whereas for giving alarm calls it was 0.392 (Table 5.5). Adult males Hari and Remo (resident adult males) both performed counterattacks more than the other adult males, though Hari shared no haplotypes with group members, unlike Remo who was a maternal sibling (Table 5.4, Figure 5.4). Other males, Viru (Type 1) and Thumri (Type 3) were newly immigrant males, but have S group haplotypes, and did not show counterattack or emit alarm calls frequently (Table 5.4, Figure 5.4). Like as has been reported at Ramnagar, these males likely left when young and returned as adults.

The ratio of the probability of choosing to counterattack over fleeing and freezing by adult males with higher grooming rates was 10.588, whereas for choosing to give alarm calls was -0.772 (Table 5.5). Adult males who received high rates of grooming from females also performed high rates of fighting with dogs, compared to males who received low rates of grooming (Table 5.5; $z=4.898$; $p<0.01$) (Figure 5.3b). Moreover, males who gave high rates of alarm calls also received high rates of grooming (Table 5.5; $z=-0.128$; $p<0.01$). Adult males Hari and Remo performed high rates of counterattack and also received high rates of grooming from females (Table 5.4, Figure 5.4f).

The ratio of the probability of counterattacking over fleeing and freezing by high-ranking males (Table 5.4, Thumri, Julio and Viru) was 0.157, whereas the ratio of probability for giving alarm calls was -0.274 (Table 5.5). Low-ranking males gave significantly more alarm calls and fought more with dogs compared to high-ranking males (Table 5.5; $z= 3.220$; $p<0.01$; $z= -6.394$; $p<0.01$) (Figure 5.3c). Furthermore, males with a high mating rate such as Viru, Thumri and Julio did not perform high rates of counterattacking and alarm calling (Table 5.5; $z=-0.130$; $p=0.880$; $z=0.832$; $p=0.053$). (Figure 5.3a, 5.4c and 5.4d).

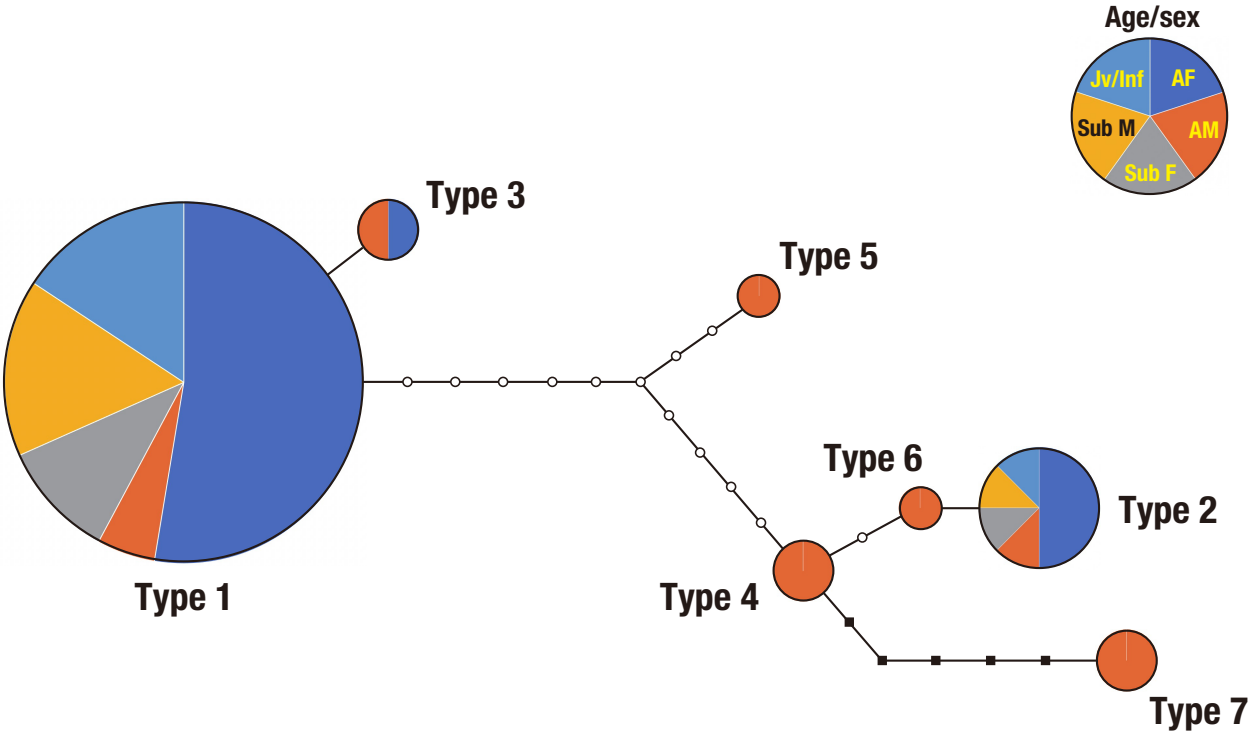

Figure 5.2. Genetic structure of the study group of the Central Himalayan langur (*Semnopithecus schistaceus*). MtDNA genealogy network was constructed by cladistic analysis based on the algorithm of Templeton et al. (1992) using the control region (1086 bp) data of 54 individuals (see Appendix Table 1). A gap was handled as the 5th state. A blank circle and a black square indicate missing haplotypes in the study group. Each step corresponds to a base substitution (○) or insertion/ deletion (■). Abbreviation of age/sex class, AF: adult female, AM: adult male, Sub F: subadult female, Sub M: subadult male, Jv/Inf: Juvenile and Infant of both sexes.

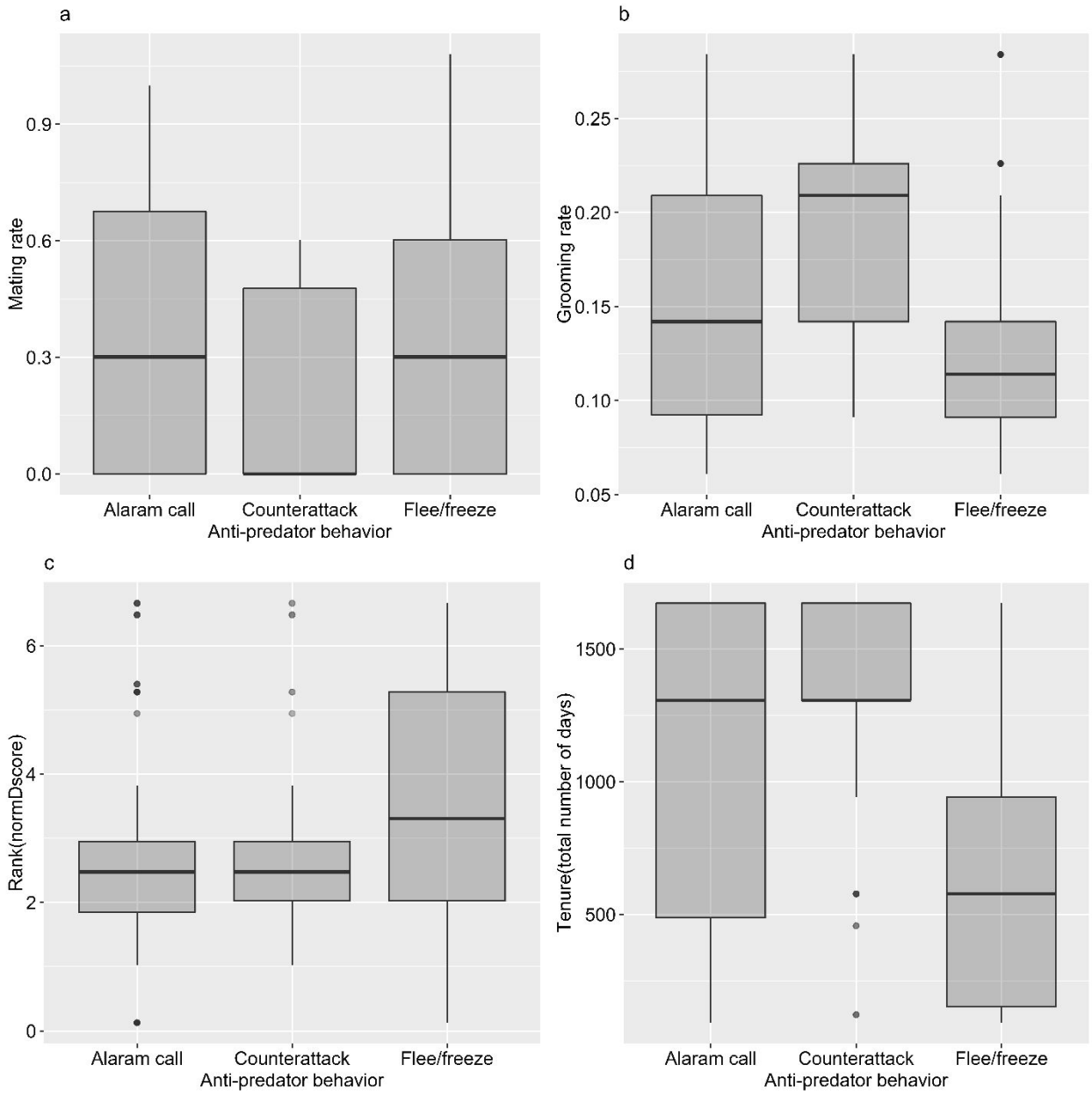

Figure 5.3. Predictor variables in relation to anti-predatory response by adult male (n= 312). The box bound the IQR (equal distance between first and third quartiles) divided by the median while the whiskers extend to a maximum of 1.5 × IQR beyond the box.

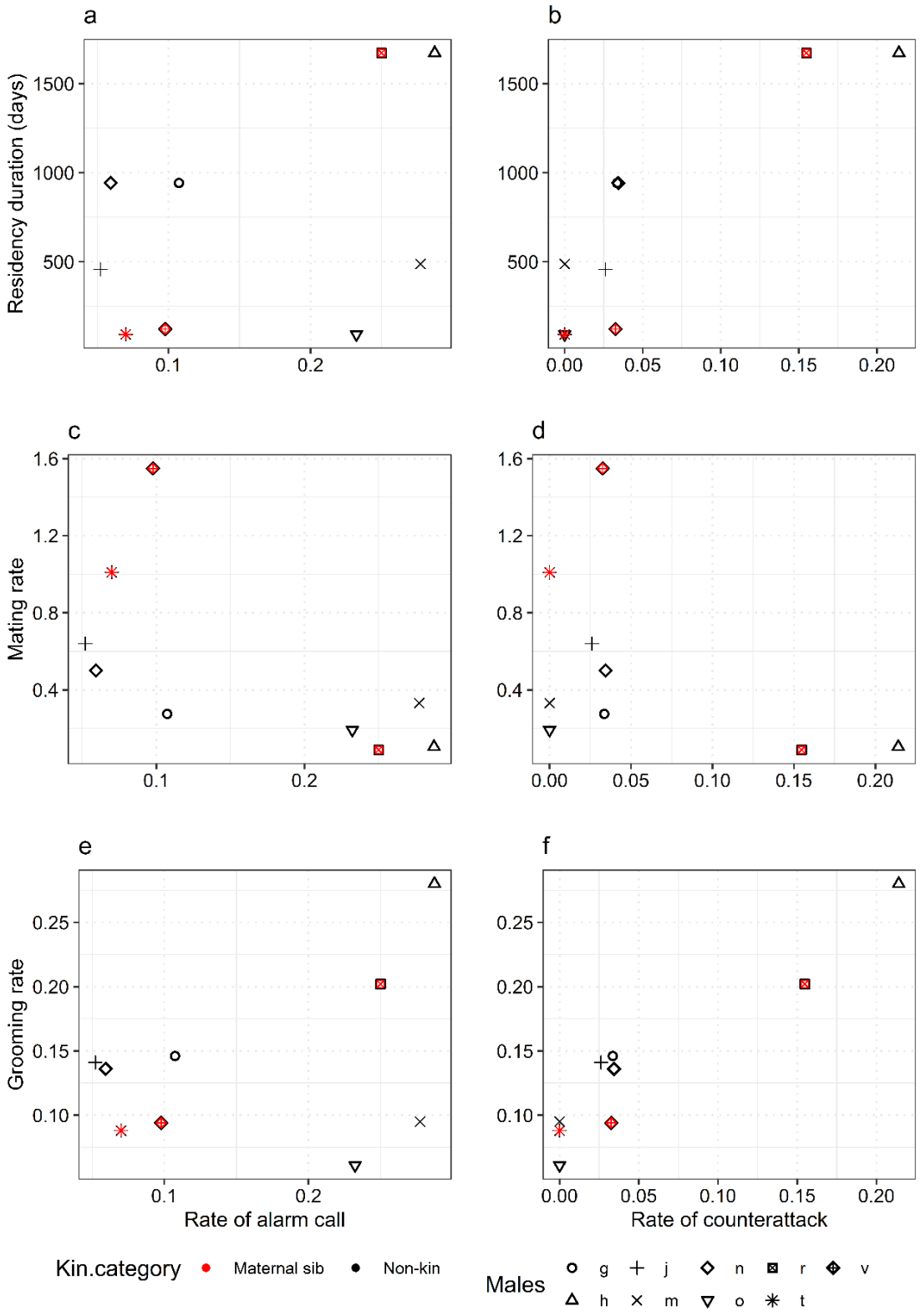

Figure 5.4. Predictor variables in relation to high cost risk taken by each adult male (n=9 adult males)

5.5. Discussion

Primate groups under predation risk is high tend to contain more males, arguably because they are needed to protect females and younger group members against predators (Cheney and Wrangham, 1987; Schaik and Hörstermann, 1994). However, it is not known if all males contribute equally to defense of the group, or take the same level of risk and why. This study investigated the behavioral strategies of adult male CHL in response to dog predation. Based on five selected attributes we tested five predictions about who is most likely to exhibit these riskier anti-predator behaviors and why. I found that while high-ranking, newly immigrant males obtained high mating success, they rarely if ever performed high-risk anti-predator behaviors. By contrast, adult males who aggressively interacted with predatory dogs tended to share the same haplotype with group females, had longer tenure in the group, and thus more experience with village dogs. These males also had strong grooming bonds with females. Anti-predatory strategies of adult male CHL were not easily explained by most of the current evolutionary hypothesis on the topic.

Although having multiple males in a group may be beneficial for females, it increases competition among males for mates (Trivers, 1972; Altmann, 1962). A study on low altitude CHL in Ramnagar, Nepal (multi-female multi-male group) showed that immigrant males had a higher chance of becoming alpha than did resident males (Borries, 2000). Moreover, these alpha males sired 57% of the new infants in the group, while resident lower-ranking males combined, sired only 27%, and the remaining infants were apparently sired by extra-group males (Launhardt et al., 2001). I was unable to determine the paternity of infants in my study group, but behavioral observations showed that high-ranking immigrant males engaged in most of the mating activity, but none of the high-risk anti-predator behaviors.

In Ramnagar, males that entered the group during the mating season and replaced the current alpha male, subsequently displayed the highest frequencies of mating activity (Borries et al., 2017). Staying in a group for a long time does not appear to provide rank-related mating benefits. This raises the question of why males stay in the same group for so long and perform high-risk anti-predator behaviors for low reproductive return. One possibility is that these males have sired offspring there and are protecting their earlier reproductive investments (Smuts, 2017). Long-term resident males, protectors of the group members against predators, are more likely than recent immigrant males to have already sired offspring in the group. Two

natal and long-term resident adult males in the study group showed high rates of direct fighting with dogs, but others males did not. Another possibility is that this kind of risk-taking behavior is linked to personality. Behavioral traits such as aggressiveness, avoidance of novelty, willingness to take risks, and exploration (Réale et al., 2007) can affect individual fitness (see Smith and Blumstein, 2008). Réale and Festa-Bianchet (2003) propose that predation pressure plays a critical role in the selection of such behavioral traits.

Also, I found that males with greater exposure to interactions with dogs through longer tenure in the group were more likely to display more aggressively, by counterattacking dogs and rescuing group members. This was revealed by the finding that these males responded more aggressively toward dogs with a history of predation on group members, than those dogs that were not normally as aggressive towards langurs. Indeed, in some animal species, anti-predatory behavior is considered a learned behavior. Indeed, in vervets (*Chlorocebus pygerythrus*) (Seyfarth and Cheney, 1980) and rhesus, predator response behavior is considered to be learned (Mineka et al., 1980). In dwarf mongoose (*Helogale undulata*), older siblings pass down anti-predator strategies to their younger sibs (Rasa, 1987).

While my observations cannot squarely address whether high-risk anti-predator behavior is learned or not, they suggest that males need time to master such high-risk behaviors if they have little or no previous experience with village dogs. Counterattacks are risky, thus newly immigrated adult males may be more unprepared to face dog attacks if they are not familiar with their behavior and the individual dogs' attitude toward langurs. Adult males living in the group for a long time (e.g. Hari and Remo) appeared to have greater understanding of predatory dog behavior, perhaps giving them more confidence to act aggressively, and come to the aid of vulnerable group members. These two males performed all of the successful rescues. Based on my unpublished data, none of the five groups sharing a boundary with S group have ever been seen in the agricultural fields, and therefore likely have little or no daily interactions with dogs. Also from observations on four other groups living in higher-altitude forests, dogs were not present there, though they have many potential predators; leopards (Ross, 1993), bears (Bishop, 1975) and mountain hawk-eagles in this area have entirely different kinds of predatory behaviors than dogs.

The exchange of grooming for agonistic support is well studied in primates. Schino (2007) evaluated 36 studies on 14 different primate species and found a positive relationship between

grooming and agonistic support. That is, individuals that groomed more also supported each other more during agonistic encounters. In this study, it was shown that males who receive more grooming from female partners also engaged more in high-risk predatory behavior (i.e. counterattack). Hari and Remo were both resident males who performed high rates of high-risk behavior and received high rate of grooming from females. The presence of long-duration resident males provides many benefits to females. White-faced capuchins (*C. capucinus* live in multi-male multi-female groups, and resident males provide benefits to females in terms of high rates of vigilance (Rasa, 1989). In Ramnagar, CHL, resident adult male langurs protect infants from attacks by newly immigrant males (Borries et al., 1999). Similarly, resident olive baboon males defend infants against aggression by immigrating males (Packer, 1979). The evolution of adult female behavioral strategies for forming social relationships can be considered in terms of inclusive fitness (direct reproductive value plus the reproductive value of one's relatives) (Wrangham, 1980). For example, chimpanzee (*Pan troglodytes*) females stay close to adult males after the birth of their offspring to gain protection against attacks on their infants by other females (Goodall, 1977). Similarly, in a one-male group of hanuman langurs (*Semnopithecus entellus*) at Mount Abu, where male group membership changes frequently, Hardy (1977) reported that females with infants preferred one male while avoiding others. In the same population, after a male takeover, females left their natal group temporarily to travel with the ousted male, and in one extreme case, attempted to follow the male who left one group to take over another. Hardy (1979) suggested that such relationships might provide protection for infants from infanticidal males.

The present study also revealed a preference for protective males: those adult males who fought with dogs were the preferred social partner for females, but not the preferred mating partner. Such males received high rates of grooming from females but were low in rank and had low rates of mating. Top-ranking adult male Julio entered the group in August 2017 and took over as alpha male. Likewise, in July-2018, Viru entered the group and took it over as the new alpha. The three top-ranking males at the time (Viru, Julio and Thumri) achieved the highest mating success of all males but performed low rates of counterattacks. Low-ranking males Hari and Remo have been living in the group at least since 2014 and showed low rates of mating, but high rates of counterattacks with predatory dogs.

It is widely accepted that male primates compete for access to fertile females, while females compete for high-quality males, access to resources, and paternal care (Emlen and Oring, 1977;

Greenwood, 1980). Affiliative bonds between adult males and lactating females are widespread in baboon societies (Lemasson, 2008; Greenwood, 1980). In olive baboons, males with strong grooming bonds with females protect these females' infants against predators and other males (Packer, 1980). It is interesting to note that social organization in the *P. anubis* is quite similar to CHL, where both live in multi-male multi-female societies with female philopatry and male dispersal. Male rank also predicts mating success and reproductive skew (Swedell, 2015). The relationship between male-female social bonding beyond the mating context in such social systems needs to be studied in more detail.

In CHL an adult female strategy might be to maintain close bonds with males who protect them and their offspring, but mate with newly incoming males. However, for males the benefits of maintaining such bonds with females remains unclear, at least from the perspective of immediate reproductive benefits. The long-term benefits for males from protecting infants they sired with group females the previous year or even farther in the past needs to be examined in the future. Also, the risk of moving to another group and not being able to enter at the top is likely to be high. For some males the best option might be to remain in a group for as long as they can: although mating less, they still have the benefits of a secure social position in the group. Also, high rates of receiving grooming from females provide indirect, health-related benefits to males. Grooming helps to remove disease- or discomfort-promoting ectoparasites (Zamma, 2002; Akinyi et al., 2013) and stimulates the production of endorphins (Keverne et al., 1989). Moreover, the hygienic function of allogrooming has been confirmed in many studies, showing a significant negative correlation between grooming rate and parasite load (Hutchins and Barash, 1976; Saunders, 1988; Grueter et al., 2013; Akinyi et al., 2013). High ectoparasite burdens are known to impact directly on host fitness (Lehmann, 1993).

Moreover, males sharing the same haplotype as group with females were more likely to take greater risks against predators to defend the group. In vervet monkeys (*Chlorocebus pygerythrus*) the likelihood of giving alarm calls is affected by kinship (Cheney and Seyfarth, 1985). However, the option to stay and protect ones' kin, with fewer opportunities to mate, is an option that high-altitude CHL living in a multi-male multi-female society have that low altitude Hanuman langurs living in single-male multi-female groups do not have. More time is needed to look at the longer-term strategies of males to fully understand the implications of these choices.

This high degree of behavioral adaptation to environmental circumstances provides insights

into the behavioral flexibility in this species. Further systematic studies on anti-predator behavior in other primate species will be helpful in expanding our understanding of the effects of human impacts on behavioral flexibility and their capability of survival in human- modified environments.

Table 5.1. Population structure and distribution of predation attempts against langurs by age sex class

Age/Sex Class	Number of individuals in 2017	Number of individuals killed by dogs	Number of individuals injured by dogs	Number of individuals in 2018	Number of individuals killed by dogs	Number of individuals injured by dogs
Infant	12	0	1	10	0	2
Juvenile	10	2	2	11	0	1
Sub adult	15	3	0	16	2	1
Adult female	28	0	0	32	1	0
Adult male	6	0	0	9	0	0
Total	**71**	**5**	**3**	**78**	**3**	**4**

Table 5.2. Description of six predictors used in the eight functional models

Predictors	**Receiving Grooming rate**	**Mating rate**	**Genetic relatedness**	**Residency duration (days)**	**Rank**
Description	Duration of grooming bouts divided by total focal duration	Count of mating divided by the total number of days male present in the group	Males related through maternal lines	Total number of days male stayed in the group	Normalized David score value
Scale	Numerical	Numerical	Yes/No	Ordinal	Numerical
Integrated	×	×	×	×	×
RD: RGr-rate	×			×	
RD				×	
RD:GR			×	×	
GR: RGr-rate	×		×		
RGr-rate	×				
MR: Rank		×			×
GR			×		
Null					

Note. *GR*: genetic relatedness; *RGr-rate*: Receiving grooming rate; *MR*: mating rate *RD:* residency duration

Table 5.3. Results from multimodal inference

Models	K	AICc	ΔAICc	Weight	Cum.weight	Log-likelihood
Integrated	12	2530.45	0.00	1.00	1.00	-1253.14
RD: RGr-rate	6	2561.92	31.48	0.00	1.00	-1274.94
RD	4	2583.28	52.83	0.00	1.00	-1287.63
RD: GR	6	2586.49	56.04	0.00	1.00	-1287.22
GR: RGr-rate	6	2636.06	105.61	0.00	1.00	-1312.23
RGr-rate	4	2641.91	111.47	0.00	1.00	-1316.95
MR: Rank	6	2703.04	172.59	0.00	1.00	-1345.50
GR	4	2795.96	265.51	0.00	1.00	-1393.97
Null	2	2802.24	271.79	0.00	1.00	-1399.12

Note. ΔAICc: difference in the AICc between the model with the lowest AICc and the following one; AICc: Akaike's information criterion corrected for small sample size; Cum. weight: Cumulative weight; *GR*: genetic relatedness; *RGr-rate*: receiving grooming rate; K: number of variables included; *MR*: mating rate *RD:* residency duration; *RS*: residency status; Weight: model probabilities

Table 5.4. Adult male characteristics

Adult males	Total observation hours	mtDNA haplotype	First reported in troop	Residency duration (Days)	Normalized David score (Rank)	Rate of behavior/day				
						Copulations	Total receiving grooming from female (minutes)	Counterattack	Alarm call	Flee/freeze
Gichu (g)	269	Type 4	May, 2016	942	4.48	0.28	8	0.03	0.11	0.81
Hari (h)	239	Type 4	June, 2014	1672	2.48	0.1	15	0.21	0.29	0.54
Julio (j)	260	Type 4	August, 2017	457	5.89	0.64	10	0.03	0.05	0.93
Muki (m)	252	Type 5	July, 2017	487	0.85	0.33	10	0	0.28	0.74
Nati (n)	276	Type 4	May, 2016	942	3.18	0.5	7	0.03	0.06	0.92
Orange (o)	109	Type 6	August, 2018	92	1.59	0.19	8	0	0.23	0.77
Remo (r)	265	Type 2	June, 2014	1672	1.75	0.09	11	0.15	0.25	0.63
Thumri (t)	119	Type 3	August, 2018	92	5.4	1.01	9	0	0.07	0.94
Viru (v)	128	Type 1	July, 2018	122	6.66	1.55	11	0.03	0.1	0.88

Table 5.5. Results from a multinomial logistic regression model with counterattack and alarm call as a response variables.

Model	Predictor variable	Counterattack			Alarm call		
		z value	p value	Coef (SE)	z value	p value	Coef (SE)
Integrated	Residency duration	12.876	**<0.01**	0.002 (0.0001)	7.134	**<0.01**	0.001 (0.0001)
	Genetic relatedness	2.085	**<0.05**	0.393 (0.188)	-0.857	0.392	-0.132 (0.154)
	Grooming rate	4.898	**<0.01**	10.588 (0.006)	-0.128	**<0.01**	-0.772 (0.020)
	Rank	3.220	**<0.01**	0.157 (0.048)	-6.394	**<0.01**	-0.274 (0.043)
	Mating rate	-0.130	0.880	-0.016 (0.118)	0.832	0.163	0.074 (0.053)

Appendix Table 5.1. Sample information of Central Himalayan langur (*Semnopithecus schistaceus*) individuals used in mtDNA sequencing. Three mtDNA regions, the control region (CR), cytochrome b (CYTB) gene and the 1.8 kb region, were examined (✓: DNA sequence data available).

Individual ID	Age/sex	DNA sample No.	**MtDNA**			MtDNA haplotype
			CR	CYTB	1.8 kb	
Abhi	AF	1	✓	n.e.	n.e.	Type 1
Abhi2	AF	184	✓	n.e.	n.e.	Type 1
Badi	AF	202	✓	n.a.	✓	Type 1
Beauty	AF	269	✓	✓	✓	Type 1
Geeta	AF	59	✓	✓	✓	Type 1
Goli	AF	251	✓	n.a.	✓	Type 1
Manu	AF	261	✓	n.a.	✓	Type 1
Meenu	AF	185	✓	n.a.	✓	Type 1
Naina	AF	201	✓	n.e.	n.e.	Type 1
Nalini1	AF	87	✓	n.a.	✓	Type 1
Nalini2	AF	103	✓	n.a.	✓	Type 1
Nani2	AF	67	✓	✓	✓	Type 2
Neelu	AF	221	✓	n.e.	n.e.	Type 1
Peeli	AF	236	✓	✓	✓	Type 3
Rohit	AF	213	✓	n.e.	n.e.	Type 1
Sahas	AF	199	✓	n.a.	✓	Type 1
Sanu1	AF	234	✓	n.e.	n.e.	Type 2
Sanu2	AF	203	✓	n.e.	n.e.	Type 1
Sanu3	AF	217	✓	n.e.	n.e.	Type 1
Shakti	AF	187	✓	n.e.	n.e.	Type 2
Soli	AF	277	✓	n.e.	n.e.	Type 1
Sukhveer	AF	242	✓	n.e.	n.e.	Type 2
Tandi	AF	255	✓	n.e.	n.e.	Type 1
Tandi jr	AF	136	✓	n.e.	n.e.	Type 1
Tashi	AF	233	✓	n.e.	n.e.	Type 1
Batman	AM	227	✓	n.e.	n.e.	Type 1
Gichu	AM	72	✓	✓	✓	Type 4
Hari	AM	4	✓	✓	✓	Type 7
Julio	AM	167	✓	n.a.	✓	Type 4
Muki	AM	110	✓	n.a.	✓	Type 5

(Continued)

Nati	AM	84	✓	n.a.	✓	Type 7
Orange	AM	276	✓	✓	✓	Type 6
Remo	AM	64	✓	✓	✓	Type 2
Thumri	AM	222	✓	✓	✓	Type 3
Viru	AM	235	✓	n.a.	✓	Type 1
Gulabo	Sub F	161	✓	n.e.	n.e.	Type 1
Gulabo2	Sub F	205	✓	n.e.	n.e.	Type 1
Leela	Sub F	173	✓	n.e.	n.e.	Type 1
Taklu	Sub F	75	✓	n.e.	n.e.	Type 2
Teenu	Sub F	219	✓	n.e.	n.e.	Type 1
Alone	Sub M	137	✓	n.e.	n.e.	Type 1
Deepika	Sub M	207	✓	✓	✓	Type 1
Deepika jr	Sub M	71	✓	n.e.	n.e.	Type 1
Nathulal	Sub M	50	✓	n.a.	✓	Type 1
Ranveer	Sub M	123	✓	n.e.	n.e.	Type 2
Special	Sub M	192	✓	n.a.	✓	Type 1
Vijay	Sub M	169	✓	n.e.	n.e.	Type 1
Unk3	JV M	112	✓	n.e.	n.e.	Type 1
Priya	JV F	206	✓	n.e.	n.e.	Type 1
Nauty	JV M	215	✓	n.e.	n.e.	Type 2
Sanu3jv	JV M	93	✓	n.e.	n.e.	Type 1
Singhania	JV M	37	✓	n.e.	n.e.	Type 1
Tarasingh	JV M	204	✓	n.e.	n.e.	Type 1
*Unk2	Inf	142	✓	n.e.	n.e.	Type 1

Abbreviation of Age/Sex, AF: adult female, AM: adult male, Sub F: subadult female, Sub M: subadult male, JVF: Juvenile female, JV M: juvenile male, Inf: infant. n.e: not examined. n.a.: not amplified in PCR, *: infant sex is not known.

Appendix Table 5.2. Distribution of 7 mtDNA haplotypes in the study group of the Central Himalayan Langur (*Semnopithecus schistaceus*) in age/ sex classes.

Age/sex	MtDNA							Total
	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	
AF	20	4	1	0	0	0	0	25
AM	2	1	1	2	1	1	2	10
SubF	4	1	0	0	0	0	0	5
SubM	6	1	0	0	0	0	0	7
Jv/Inf	6	1	0	0	0	0	0	7
Total	38	8	2	2	1	1	2	54

Abbreviation of age/sex class, AF: adult female, AM: adult male, Sub F: subadult female, Sub M: subadult male, Jv/Inf: Juvenile and Infant of both sexes

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CHAPTER 6

GENERAL DISCUSSION

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Chapter 6

General Discussion

6.1. Overview

Central Himalayan langur (CHL) females showed distinct patterns of social interactions in relation to their rank, age, kinship, group membership status (natal, immigrant) and presence or absence of dependent offspring. This study represents an unusually detailed account for any species in the genus *Semnopithecus* (8 species; Roos et al., 2014) for the social and genetic structures of females in a group, and the presence of immigrant females forming two distinct haplogroups different from most of the group members. High-ranking females had a greater number of grooming partners, and others groomed females with infants for longer durations. Such strong bonds are known to be beneficial for infant survival. Natal subadult and immigrant (having extra-group haplotype of mtDNA) females formed strong indirect connections, greatly facilitating the overall social connectivity of group members. Immigrant females formed strong grooming relationships with females who themselves had strong bonds, a trait linked in other species to increased fitness (Chapter 2). Furthermore, CHL patterns of interactions with humans and predators appeared to be adapted to maximize fitness.

Interactions with local people were complex. When foraging in and around agricultural fields in the village, langurs frequently encountered humans and dogs. Low availability of dense oak (*Quercus leucotricohophora*) patches for sleeping sites by langurs seemed to be one reason for their intense feeding on agricultural crops. This relative lack of suitable sleeping trees is partly attributable to the high dependency of local farmers on this tree species for their livelihood (Chapter 3). In contrast, in high-altitude oak forest, CHL formed feeding associations with another potential predator, the Himalayan black bear (*Ursus thibetanus*). The two species shared the alpine habitat only during the peak of the fruiting season of the oak, lasting only a few months before the onset of winter. Both species needed this limited resource to store fats for the winter months ahead (Chapter 4). The study group lower down in the village habitat frequently foraged in and around the agricultural fields. This was the context for encounters with predatory dogs, which frequently

harassed and sometimes fatally attacked and ate the langurs in the fields. In response to dog attacks, longer-tenured adult male langurs took a leading role in direct counterattacks, rescuing females and infants stranded in the fields and treeless surrounding areas. Newly immigrated males took fewer risks (Chapter 5).

6.2. Functional significance of female social bonds

6.2.1. Hanuman langur female social relationships

A detailed account of female Hanuman langur (*Semnopithecus* spp.) social relationships is available from three long-term field sites, Jodhpur and Mount Abu for *S. entellus* and Ramnagar, Nepal for *S. schistaceus*. All three sites are located in the lower elevation range of the genus' distribution. Jodhpur and Mount Abu langurs mainly form one-male multi-female groups (Hardy, 1977; Borries, 1993), while the Ramnagar group has a multi-male multi-female social organization (Koenig and 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 being the lowest ranking (Hardy and Hardy, 1976). These high-ranking females' infants were more likely to survive until 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). Those findings are based on observations of multiple groups. The present long-term study on the high-altitude population of the CHL in Mandal valley, Uttarakhand, Garhwal Himalayas revealed a different pattern. I did not find an age-inverted dominance structure; in fact, young females, below the age of 6 years (subadult), were the lowest-ranking females, while fully adult and older females were the highest-ranking. CHL females tended to rise in rank after 6 years of age, when they gave birth to their first offspring (N = 4, 55 months). High-ranking females with infants had many grooming partners, and their grooming sessions tended to be longer, a characteristic which has been linked to direct fitness benefits in other primate species (Silk et al., 2003). Subadult females made more indirect connections with other group members, such as grooming with 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. It is possible that subadult females' indirect connections facilitate their rise in rank in the future, which in turn can be directly linked to reproductive success.

6.2.2. Predation and female social structure

I found that subadult females form strong indirect connections ("high betweenness centrality"), and thus appear to be the key age group in holding together the social organization and structure of CHL. High betweenness individuals connect individuals that do not interact with each other (Freeman, 1977). The disappearance of such individuals from the social network can lead to social network and group fragmentation (Holme et al., 2002; Flack et al., 2006; Lusseau, 2007). Over two years, I recorded eight deaths due to predatory attacks by dogs, and subadults were the age-class most at risk (n = 5 individuals). Old and prime adult females and juveniles feed together, with adult males tending to feed nearby. Agricultural fields on the edge of the forest were most frequented by the langurs, who typically waited for opportunities to enter and return quickly after feeding on crops. Sometimes subadults went into the crop fields on their own, while the rest of the troop stayed inside the forest. Most of the successful attacks by dogs happened during such forays, when adult male langurs were not present to protect the subadults. At the current predation rate, it is possible that there will be a significant loss of members of this age group. How will this impact the social structure of females? This issue needs to be included in an overall appraisal of the effect of predation on CHL social structure.

Ecological factors such as predation pressure and foraging behavior affect how conspecifics interact with each other (Krause et al., 2002). Conceivably, high predation pressure could be impacting CHL females' pattern of association. In the present study it was revealed that immigrant females (the type 2 haplotype group) have higher eigenvector centrality values, i.e., they are linked strongly to more individuals who are strongly linked with each other. These particular haplotype females are few (n = 6), therefore obtaining a secure central position in a social network could provide them with greater protection from predatory dogs, due to having more individuals nearby. In some species, like the chacma baboon (better to be insert the species name) (Ron et al., 1996), when the risk of predation is high, females compete over protected spatial positions rather than

access to food resources, because being near others increases the chances of detecting a predator, receiving active protection and joining with partners to mob predators. This might apply to CHL as well. The results from male-female grooming interactions show that adult males, who have stronger grooming bonds with females, will directly confront and counterattack predatory dogs. Therefore, for immigrant females it should be advantageous to acquire a central spatial position in the group and stay near other females, who themselves have more social partners, and protective adult males.

6.3. Key resource loss, crop foraging and livelihood

Dogs prey on langurs that enter into agricultural fields where the canopy cover is scarce, leaving few options for a quick escape when caught far from the forest edge. The present study showed that crop foraging by langurs in the human-dominated landscape is associated with the loss of oak, a key resource inside the forest. Similar situations have been reported for other primate species, such as red colobus (*Procolobus kirkii*) feeding more on coconuts in areas where natural food availability is low in relation to colobus density (Siex and Struhsaker, 1999). Crop feeding is also observed during seasonal shortages of key natural food species. Three primate species, red tail monkeys (*Cercopithecus ascanius*), olive baboons (*Papio anubis*) and chimpanzees (*Pan troglodytes*), feed more on bananas when wild fruit availability is low in the forest (Naughton-Treves et al., 1998). Similarly, chimpanzees feed more on other agricultural crops during periods of wild fruit scarcity (Naughton-Treves et al., 1998; Yamakoshi, 1998).

The langur groups that I observed living both near and far from the village made heavy use of oak species at certain times of the year. Oak patches were found to be critical for Mandal langurs as both sleeping and foraging sites in their home range, which overlapped with agricultural fields. In higher-altitude groups farther away from human habitation, oak was a critical source for winter survival during the fruiting season. Oak is also a principal resource for local people in the Himalayas. Excessive dependence of local communities on oak forest for use as grazing lands, removal of branches for fodder and fuelwood, leaf litter removal for use as cattle bedding and as agricultural fertilizer have severely affected the regeneration of this species, with a major effect being forest degradation (Gupta and Singh, 1962; Saxena and Srivastava, 1973; Singh and Singh,

1987; Rathore et al., 2018). This study found that CHL living near villages do not utilize their home range equally, selecting high-density oak patches as sleeping sites more over low-density patches, which led them to frequently visit agricultural fields located nearby. Although people living near degraded oak forests did not report damage from crop foraging by langurs, they did see langurs as being a serious threat. Degradation of the nearby forest, in terms of forest resource loss reported by people was due to their own high dependency on oak for their livelihoods. Thus the balance between poverty and environmental protection can only be achieved through sustainable livelihoods (McElwee, 2010). I found that people with low agricultural production depended more on livestock as an extra source of income. Their high dependency on the forest for grazing and fodder for their cattle was the leading cause of oak forest degradation.

6.4. Conservation challenges

As oak forests appear critical for CHL survival, maintaining sufficient density of oak patches is important for the conservation of this species. Poor regeneration of oak is the biggest challenge facing conservation of oak forests. This issue in the Himalayas has been reported by foresters for more than 50 years (Troup, 1921; Saxena and Singh, 1982; Singh and Singh, 1986, 1992). High densities of human and cattle in the altitudinal-ecological zone where Banj oak dominates, subject the forests to intense pressure from fuelwood collection and grazing (Mohan and Puri, 1955), and has been cited as a chief cause for low oak regeneration (Singh and Singh, 1992). Moreover, in the western Himalayas, oak-cleared forests are frequently replanted with pine species, and research indicates that the greater nutrient loss and nitrogen-poor soil brought about by pine makes it difficult for oak to re-emerge in such disturbed areas (Singh et al., 1984).

As natural regeneration is difficult in such areas of high human pressure, intervention with the careful replanting and protection of oak trees is imperative. In my study site, part of the CHL habitat (highly degraded oak patch) has been already replaced by pine. But, restoration of the oak forest alone is not sufficient for conserving the langurs, because this will not stop people's dependency on oak. For a long-term solution, sustainable livelihood alternatives must be considered. In this study, I showed that the high number of livestock maintained for marketable milk production is the leading cause of villagers' high dependency on the oak forest. Providing

alternative income sources through other activities, like ecotourism, cultivation of medicinal plants, and traditional handicraft production could reduce over-exploitation of the surrounding forest.

6.5. Female-male relationships in relation to predation pressure

6.5.1. Costs and benefits of male residency

Primate groups where predation risk is high tend to contain more males, who are needed to protect females and younger group members against predators (Cheney and Wrangham, 1987; Schaik and Hörstermann, 1994). I found that it was predominately adult males that performed anti-predator behavior. Males exhibited a variety of different antipredator strategies based on individual circumstances. Those who had lived in the group since the study began in 2014 were particularly likely to aggressively counterattack dogs, whereas resident and recent immigrant males mostly gave alarm calls. Although having multiple males in a group is beneficial for females in this way, it increases competition among males for mates (Trivers, 1972; Altmann, 1962). A study on *S. schistaceus* in Ramnagar, Nepal (multi-female multi-male group) showed that males disperse when they are subadults. When they entered a new group, these immigrant males had a higher chance of becoming alpha than did resident males (Borries, 2000). Moreover, these alpha males sired 57% of the new infants in the group, while resident lower-ranking males combined sired only 27%, and the remaining infants were apparently sired by extra-troop males (Launhardt et al., 2001). I was unable to determine the paternity of infants in my study group, but behavioral observations showed that high-ranking immigrant males engaged in most of the mating activity. In Ramnagar as well, males entered the group during the mating season, replaced the current alpha male and displayed the highest frequencies of mating activity (Borries et al., 2017). Staying in a group for a long time does not appear to provide rank-related benefits. However, this raises the question of why males stay in the same group for so long and perform high-risk anti-predator behaviors for low reproductive return. One possibility is that these males have sired offspring there and are protecting their former reproductive successes (Smuts, 2017). Two natal and long-term resident adult males in the study group showed high rates of direct fighting with dogs, but others males did

not. Another possibility might be that this kind of risk-taking behavior is linked to personality. Behavioral traits such as aggressiveness, avoidance of novelty, willingness to take risks, and exploration (Réale et al., 2007) can affect individual fitness (see Smith and Blumstein, 2008). Réale and Festa-Bianchet (2003) propose that predation pressure plays a critical role in the selection of such behavioral traits. Whether predation is a factor favoring the expression of boldness in CHL should be evaluated in the future.

6.5.2. Female behavioral strategies

The presence of resident males provides many benefits to females. White-faced capuchins, *Cebus capucinus* live in multi-male multi-female groups. Resident males provide benefits to females in terms of high rates of vigilance. In Nepal, resident adult male langurs protect infants from attacks by newly immigrant males (Borries et al., 1999). Resident olive baboon males defend infants against aggression by immigrating males (Packer, 1979). An important determinant of mating partner selection by females may be a male's ability to protect her infants from infanticide (Hrdy, 1979). The evolution of adult female behavioral strategies for forming social relationships can be considered in terms of inclusive fitness (direct reproductive value plus the reproductive value of one's relatives) (Wrangham, 1980). For example, chimpanzee females stay close to adult males after the birth of their offspring to gain protection against attacks on their infants by other females (Goodall, 1977). Similarly, in a one-male group hanuman langur population at Mount Abu, where male group membership changes frequently, Hardy (1977) reported that females with infants preferred one male while avoiding others. In the same population, after a male takeover, females left their natal troop temporarily to travel with the ousted male, and in one extreme case, attempted to follow a male who left one troop to take over another. Hardy (1979) suggested that such relationships might provide protection for infants from infanticidal males.

My data also revealed a preference for protective males, that is those adult males who fight with dogs were the preferred social partner for females, but not the preferred mating partner. Such males had more grooming partners and stronger grooming bonds. However, it is widely accepted that males compete for access to fertile females while females compete for high-quality males, access to resources, and paternal care (Emlen and Oring, 1977; Greenwood, 1980). Affiliative bonds

between adult males and lactating females are widespread in baboon societies (*P. hamadryas* subsp.) (Lemasson, 2008; Greenwood, 1980). In olive baboons, males with strong grooming bonds with females protect the latters' infants against predators and other males (Packer, 1980). In CHL it could be the adult female strategy to maintain close bonds with males who protect them and their offspring. However, for males the benefits of maintaining such bonds with females remains unclear, at least from the perspective of immediate reproductive benefits. Possible long-term benefits for males from protecting infants they sired with group females the previous year or even farther in the past needs to be examined in the future.

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