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ORIGINAL ARTICLE

Anti-predator strategies of adult male Central Himalayan Langurs (*Semnopithecus schistaceus*) in response to domestic dogs in a human-dominated landscape

Himani Nautiyal[1,2,5] · **Hiroyuki Tanaka**[1,3] · **Michael A. Huffman**[1,4]

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Abstract

The evolution of predator–prey relationships is an important topic in primatology. 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 exist on the subject. Furthermore, little information exists regarding the inter-male variation in responses to predators. To address this data gap, 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. We recorded 312 langur–dog interactions over 2 years. These predation events resulted in 15 serious attacks on adult females, infants, juveniles and sub-adults, in eight of which the prey was killed and consumed on the spot. In response to dog predation, adult males performed three types of anti-predator response behaviors: direct fighting with a predator, emitting alarm calls, fleeing and/or freezing. Differences were noted in each male's response to village dogs. The results showed that the likelihood of CHL adult males engaging in more costly counterattacks or attention getting alarm calls were better predicted by the level of investment in the group (genetic relatedness, duration of residency, social relationships), but not rank and mating rate. Long-duration resident adult males performed high and/or intermediate cost behaviors to protect vulnerable members of the group; their potential offspring, maternal siblings or cousins, and adult female social partners. Short-term residents or recent immigrant males exhibited two less energetically costly, more self-preserving behaviors, depending on their rank: (1) high-ranking short-tenure duration males, with high mating frequencies, performed flee and freeze responses; (2) low-ranking, low-mating-frequency males performed more alarm calls. Counterattacks and alarm calls were performed by adult males with relatively more experience with village dogs and were directed towards dogs with predatory histories significantly more often than dogs with non-predatory histories. Natural selection and kin selection have both contributed to the evolution of CHL anti-predator tactics.

Keywords Anti-predation strategy · Dog–wildlife interaction · mtDNA haplotype · Crop foraging

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 considered to be an important factor responsible for the evolution of primate societies (Cheney and Wrangham 1987). Indeed, primates have many types of predators: in one review, 174 predator species were recognized (Hart 2007). However, most previous studies on primate predator–prey interactions are lacking in great detail, because systematic observations of such rare events

✉ Himani Nautiyal
himani.nautiyal08@gmail.com

1 Kyoto University, Primate Research Institute, Inuyama, Aichi, Japan

2 National Institute of Advanced Studies, Indian Institute of Science, Bengaluru, India

3 Center for Ecological Research, Inuyama Campus, Kyoto University, Inuyama, Aichi, Japan

4 Wildlife Research Center, Inuyama Campus, Kyoto University, Inuyama, Aichi, Japan

5 Sangam Vihar Chauras, Kilkileshwar, Tehri Garhwal, Uttarakhand 249161, India

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are difficult in the wild (Stanford 2002). A general review of the evidence gathered thus far is presented by Miller and Treves (2007).

Anti-predation strategies are widespread among animal taxa and act largely to diminish the cost of being pursued or captured by a predator. One strategy is to emit alarm calls in the presence of predators; these warn nearby conspecifics about the potential threat and occur in almost all primate species (Bishop 1979; Cheney and Wrangham 1987; Curio 1978; Zuberbühler 2000). Some primate species are known to confront predators directly, by what is known as 'mobbing' or 'counterattacking' (Crofoot 2012; Tórrez et al. 2012). Such aggressive defense against predators is often reported in multi-male primate societies (Stoltz and Saayman 1970; Boinski 1988; Jones et al. 2006). Individuals engaged in such active defense should perceive this behavior as stressful and risky (Arlet and Isbell 2009), yet some select it over the less costly predation response freeze and/or flee. Anti-predator strategies such as alarm calling or counterattacking are considered to be energetically costly and more conspicuous behaviors (Curio and Regelmann 1986; Poiani and Yorke 1989; Motta-Junior 2007; Cunha et al. 2017) due to the potential for bodily harm or drawing unwanted attention toward oneself. Moreover, Dugatkin and Godin (1992) suggested six major costs of antipredator behavior: increased risk of mortality to self, increased cost of mortality to relatives, lost mating opportunities, lost feeding opportunities, energetic costs of approaching a predator, and costs of being exploited by others. Although the likelihood of being killed by a predator during a counterattack may be relatively low, if realized, the outcome is absolute. For instance, primates mobbing predatory leopards and jaguars have been killed (Cowlishaw 1994; Tórrez et al. 2012). Over the long run, even if not resulting in fatalities, the energetic costs of performing mobbing, counterattacks and alarm calls, maybe minor most of the time, 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 and/or intermediate cost behaviors. Such hypotheses have been tested in a variety of different taxa (Dugatkin and Godin 1992; Maklakov 2002), but only a handful of studies have looked at this aspect in primates (Cheney and Seyfarth 1981; 1985; Zuberbühler et al. 1999; Wheeler 2008).

The "*parental care*" hypothesis posits that individual anti-predatory behavior may benefit offspring by alerting them to the presence of predators. For this to be effective, males must perform such behaviors in a way that will increase the chances of their potential offspring's survival, and consequently their own fitness (Williams 1966; Wheeler 2008). This may occur when males with longer tenure provide anti-predator services to former mating partners and their offspring (Van Schaik et al. 2021). The 'kin selection hypothesis' posits that animals help others with whom they share genes by common descent, promoting the spread of those genes within the population (Hamilton 1964). In primates, the role of kin selection has been studied with regard to social grooming and coalition formation, but considerably less attention has been paid to anti-predatory responses (Silk 2002). The 'reciprocal altruism' hypothesis suggests that an individual may perform a costly act that benefits another unrelated individual, and will be repaid in the future (Trivers 1971). However, many examples of altruistic behavior in the literature are debatable, due to the low cost to the actor (Clutton-Brock 2002; Schino 2007). High and/or intermediate cost behaviors such as direct encounters with a predator might provide clearer support for 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, 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). For example, white-throated magpie-jays (*Calocitta formosa*) use predator interactions to advertise their presence and availability as potential mates (Ellis 2009).

Domestic dogs (Canidae) are the most globally abundant and widely distributed carnivore species, and India has one of the largest dog populations of any country (Gompper 2014; Doherty et al. 2017; Ritchie et al. 2013). Dog predation on primates is mostly reported in 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 (*Theropithecus gelada*) in the open highland grasslands of Ethiopia (Iwamoto et al. 1996). These landscapes are defined as being human-modified and are comprised of forest patches surrounded by agricultural land and settlements. Moreover, crop foraging is risky behavior, as animals are exposed to unfavorable circumstances resulting in injury or death from people and dogs sent out to protect their crops from wild animals (Hill 2018).

The Central Himalayan Langur (*Semnopithecus schistaceus*) (CHL) living in human dominated-landscapes is reported to forage on crops that result in frequent encounters with domestic dogs and people (Nautiyal et al. 2020). Some of these same dogs are also used to protect livestock from leopards that live and hunt at the edges of the villages and up in the high alpine meadows where livestock range during the summer months (Nautiyal et al 2020). We took advantage of this situation to better understand primate anti-predator behavior and the possible costs and benefits incurred by the CHL in this study, 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 sometimes 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).

To elucidate the costs and benefits associated with adult male langur anti-predator behavior, we investigated the relationships among the type of anti-predatory behavior displayed (high cost: counterattack, intermediate cost: alarm calls; low cost: flee-freeze), adult male attributes (rank, group residency duration, genetic relatedness to the group), and potential social benefits (mating, grooming) obtained by these males. Based on existing anti-predation hypotheses and information about langur behavioral ecology presented above, we test five predictions (Table 1).

Materials and methods

Study site and population

The research was conducted on the S group in Mandal valley, Chamoli, Uttarakhand, Garhwal Himalayas, India (1500–1800 m above sea level) from May 2017 to November 2018 (details of the S group are described in Table 2). The study group home range overlaps both agricultural fields and forests, placing them frequently in close proximity to humans and domestic dogs. This group feeds on crops and fodder trees inside the agricultural fields at certain times of the year (Nautiyal et al. 2020). Village dogs are allowed to roam freely to guard their fields from crop-foraging wildlife. Under these conditions, the S group risks encounters with domestic dogs whenever they enter the agricultural fields, thus crop foraging and the

Table 1 Hypotheses and predictions of the study

Hypothesis	Predictions	Predictor variables	Scale	Supports the hypothesis
Parental care	Longer-tenured males, potentially having more offspring in a group, will perform more energetically costly behaviors than males with shorter residency and less possibility of offspring or other possible investment in group members	Residency duration (days)	Ordinal	Yes
Kin selection	Males with more female kin relatives in the group will perform more energetically costly behaviors than males with no relatives in the group	Genetic relatedness	Yes/no	Yes
Reciprocal altruism	Males that exhibit energetically costly behaviors will have strong grooming bonds with females	Receiving grooming rate	Numerical	Yes
Costly signaling	Low-ranking, newly immigrant males will perform more energetically costly anti-predator behaviors	Rank	Numerical	Yes
	Males that exhibit energetically costly behaviors will have higher mating rates	Mating rate	Numerical	No

Table 2 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**

Bold values indicates the total of each column

serious threat to all group members of predation by dogs are inextricably linked. 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 (see Nautiyal 2015 for further details of the study site).

Behavioral data collection

Data were collected on all nine adult males when each was present from May 2017–November 2017 and June 2018–November 2018. The group was followed from 06:00 to 18:00 each day, on average for 25 days per month. Individuals were identified by their 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 two assistants, PB and HM) were present at the study site. Inter-observer reliability of identification was assured by testing identifications using the photo catalog. HN and one assistant collected focal samples for male grooming and mating behavior. Additional information was obtained after the end of this study by trained observers, and local support staff in the village, on additional langur–dog interactions mentioned below but not included in the analyses.

In total, 1917 h (mean 213 ± 23.89 SE hours per male) of focal observations (15 min per session) of the nine adult males were recorded. For focal observations, adult males were chosen randomly, and observations were balanced across the time of day. 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 study was conducted mostly during the mating season of both years when non-natal males was entering or leaving the troop. The presence and absence of all males were recorded each day. Male–male dyadic displacement interactions for rank analysis were collected from ad-libitum data (Altmann 1974).

Dog–langur interactions primarily happen at the forest edge and in the agricultural fields. 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, and also the dogs' encounters with other group members ad libitum (Altmann 1974) until the dogs left or were effectively chased away by the langurs. All adult males remain near the entire group when they enter the agricultural field from the forest. Some males give alarm calls, some fight with dogs, and this behavior continues for a few seconds. This gives observers enough time to record the responses because of the clear visibility of all males in this open landscape. Adult male langurs would sometimes actively chase approaching dogs away, that fled back to the village, typically keeping them from approaching the group again for at least 30 min or more. The distance chased was not always clear, as sometimes dogs came from the village even when langurs were some distance away, but other times they would come when the langurs were within 100 m of the village. In some cases, villagers were also present during such encounters. Dogs were fully habituated to human presence and observers remained neutral during such encounters; thus, human presence did not affect the outcome of dog–langur encounters. For analysis, we divided langur responses into three categories: 'alarm call', 'counterattack', and 'flee and freeze'. Each encounter was written down in a notebook and some were video recorded. Each male was scored as producing just one type of response for each encounter.

Predator information

Dogs were individually identified based on their body size, sex, and coat color. These free-roaming dogs are owned by the villagers within the S group territory. Dogs involved in interactions with langurs more than once were included in the observations. Based on these interactions, 12 village dogs were classified either as a predator ($n = 5$) or a non-predator ($n = 7$). Dogs that predate on langurs are those individuals that have a history of killing and eating or injuring langurs in the past. Dogs that do not, have only been observed to be involved in chasing langurs from the agricultural fields, but never injuring, killing or eating them.

Behavioral definitions

Alarm calls of Himalayan langurs (*S. ajax and S. schistecaus*) are defined as multiple-phase bark or bark threat call (Bishop 1979). They are typically given when a potential predator is detected. We noted that males gave alarm barks only when dogs approached the troop or chased a troop member (see Supplementary Video 1). In response to alarm calls, other individuals became alert, vocalized, or fled the area, stopping other activities, such as grooming, mating, feeding, or playing. Counterattack is defined as aggressive behavior directed at a dog (Crofoot 2012). Langur aggressive behavior includes a combination of such behaviors as aggressive slap, push, bite and pull, often accompanied by an aggressive grunt (see Supplementary Video 2). Flee and/or freeze behavior is defined as the escape from the ground up into a nearby tree when a dog approaches, where they then silently sit still. Males already in the trees when a dog approaches tend to remain silently still. In this way, they avoid any interactions with the dog. Mating behavior included copulation, and sexual solicitations resulting in a

male mounting a female followed by pelvic thrusting (Sommer et al. 1992). 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). Dyadic interactions are defined as one individual physically displacing another (Hrdy and Hrdy 1976). Adult males staying in the troop for more than one mating season were called residents, and those present for less than one mating season were classified as immigrants.

Noninvasive sample (feces) collection and mitochondrial 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 in a total of 54 individuals (69% of all the members of the study group), including all adult males (see Supplementary Material 1). Fecal samples were collected only when the identity of the individual could be directly assigned to the sample. After DNA extraction, the control region (CR) and the cytochrome b gene (CYTB) were examined to detect intraspecific variation in the CHL. These two regions of mtDNA were amplified by PCR using three different primer pairs which amplify the full length of CR and 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, 23 (11 adult females, nine adult males, and three subadult males) were selected for analysis of sequences obtained using the three primer pairs mentioned above since it was expected that all the haplotypes of the study group would be detected from those individuals when considering the langurs' life history. The remaining 31 individuals were examined for CR. Classification of mtDNA haplotypes was carried out by aligning DNA sequence data using Sequence Navigator (Applied Biosystems) and GENETYX-MAC software packages. For detailed procedures of the DNA work, see Supplementary Material 2. The genetic structure of the study group was reconstructed using the CR data (1086 bp) of 54 individuals (Supplementary Material 3). 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). The frequencies of mtDNA haplotypes in each age/sex class were also totaled.

Study variables

Residency duration was scored as the total number of days an adult male stayed in the 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 this study from 2014 to 2018; the others appeared at different times during the study period. Genetic relatedness was assigned based on haplotype sharing with female group members (related or not related). The mating rate of each male was based on the total number of copulations performed divided by their total observation hours. The grooming rate was based on the total grooming hours for each adult male divided by the total observation hours. Dominance rank was determined using David's score (David 1987) based on 3531 dyadic interactions. For the analysis we calculated David score value separately for each year for each adult male. However, the final rank value presented in Table 4 was calculated using the mean David score over 2 years for each male.

Model formulation and statistical analysis

To examine the potential benefits of performing high and/or intermediate cost anti-predator behavior, multinomial logistic regression (MLR) analysis was performed using *the nnet package* (Venables and Ripley 2002) in R, version 3.5.3 (R Core Team 2019). MLR is an extension of binary logistic regression that allows for more than two categories of dependent variables. Like binary logistic regression, MLR uses maximum likelihood estimation to evaluate the probability of categorical membership, in which the log odds of the outcomes are modeled as a linear combination of the predictor variables (Anderson and Rutkowski 2008). The model estimates a separate set of parameters called regression coefficients (log odds) for each level of the dependent variable.

Alarm calls possibly draw attention to the caller, the level of risk is significantly less compared to males that counterattack, but potentially riskier than males that display flee and/or freeze. Therefore, we categorized outcome variables based on the magnitude of the cost associated with anti-predatory responses: the high cost for a counterattack, the intermediate cost for an alarm call and, the low-cost for flee and/or freeze. In MLR, log odds estimate the relationship between predictor variables and the probabilities of each of the categorical outcome variables (three types of anti-predator behavior) relative to the reference category. The log odds of high and/or intermediate cost behavior over low-cost behavior were used to express the effect of predictors with low-cost behavior (flee and/or freeze) as the baseline for all models. A log ratio larger than one indicates that the odds of being in the category increase with a one-unit increase in the predictor variable, whereas a log odds less than one shows that the odds of being in the category fall with a one-unit increase in the predictor variable. The presence of all adult males was not similar across the 2 years. To control for this, year was included as a random factor in all models. In R, we

ran tests for homogeneity of residuals and variance inflation factors (VIF) below or around 1 (Field et al. 2012).

We identified five predictor variables (defined above) to test the four hypotheses outlined in Table 1 and built one specific model for each of the four hypotheses. Parental care, kin selection and reciprocal altruism hypotheses have a single predictor, the costly signaling hypothesis has two predictors, and the integrated model includes a combination of the five predictors. We also tested the interaction between male id and all predictor variables, using male id as a fixed factor. Since the hypotheses are not mutually exclusive, we combined the hypotheses within eight statistical models (Table 3). To compare all models simultaneously, we used an information theory approach based on Akaike's information criterion (IT-AIC) to extract the best model to explain the benefit of high and/or intermediate cost behavior by males during predator encounters (Burnham and Anderson 2002; Burnham et al. 2011; Symonds and Moussalli 2011; Richards et al. 2011). In recent years, an information-theoretic (IT) approach to model-based inference has become increasingly popular across the field of ecology and behavior (e.g., Johnson and Omland 2004; Whittingham et al. 2006; Garamszegi et al. 2009; Grueber et al. 2011; Dubuscq et al. 2016; Giam and olden 2016; Mercier et al. 2017). Such model selection criteria enable formal inference from more than one model (Johnson and Omland 2004). The principle of this approach relies on a ranking of the model from the candidate set of models using ΔAICc values ($\Delta i = AIC_{c(i)} - AIC_{c(min)}$) (Burnham and Anderson 2002). The probability that a given model is the best among those in the set of models is expressed as standardized model weights (Table 3). Note that any comparison of multiple models in this framework is relative, not absolute; that is, if a model is identified as the best model, this model is considered the best one in the candidate set (Anderson, 2008). Using the "aictab" function from the package *AICcmodavg*, we measured the model Akaike's weight, or relative likelihood, and accumulative weight of each model that indicates the extent to which one model is more likely than another in explaining the variance in the data (Mazerolle 2016).

We measured a dyadic dominance index with the R package *steepness* to calculate David score values, which is associated with rank order for each adult male (Vries and Vries 2014). Moreover, we used Spearman's rank correlation coefficient to examine possible relationships between adult male attributes (Sokal and Rohlf 2012).

Table 3 Model characteristics explaining benefit of anti-predator behavior

MLR models	K	AICc	ΔAICc	Weight
Integrated				
MLR ~ RD*ID + GR*ID + MR*ID + Rank*ID + RGr-rate*ID + (1|year)	48	2492.70	0.00	1
Parental care: reciprocal altruism				
MLR ~ RD + RGr-rate + (1 year)	6	2561.92	69.23	0
Parental care				
MLR ~ RD + (1| year)	4	2583.28	90.58	0
Parental care: kin selection				
MLR ~ RD + GR + (1| year)	6	2586.49	93.79	0
Kin selection: reciprocal altruism				
MLR ~ GR + RGr-rate + (1| year)	6	2636.06	143.36	0
Reciprocal altruism				
MLR ~ RGr-rate + (1| year)	4	2641.91	149.21	0
Costly signaling				
MLR ~ MR: Rank + (1| year)	6	2703.04	210.34	0
Kin selection				
MLR ~ GR + (1| year)	4	2795.96	303.26	0
Null				
MLR ~ 1 + (1| year)	2	2802.24	309.54	0

Weight: model probabilities. An asterisk * refers to an interaction term

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, *ID* adult male identity, *K* number of free parameters in the model, *MR* mating rate, *RD* residency duration

Results

Dog–langur encounters, predation, and adult male anti-predatory defense

During the study period, a total of 1971 adult male langur responses were observed during 312 dog–langur encounters (see Supplementary Videos 3 and 4 for examples). As a consequence of these encounters, in 2017, five (7%) of the 71 group members were killed and three (4%) were injured. In 2018, three (4%) of 78 troop members were killed and four (5%) were injured (Table 2). In these eight observed langur deaths by dogs, the prey was consumed on the spot, immediately (Fig. 1).

Of these 1971 responses, alarm calls were directed towards the dogs and conspecifics 327 times, of which 65% were directed towards predatory dogs and 35% towards non-predatory dogs. Counterattack responses were observed 155 times, of which 75% were directed towards predatory dogs and 25% towards non-predatory dogs. Flee and/or freeze responses were observed 1489 times; 53% were in response to predatory dogs and 47% 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 a predator or not ($\chi^2 = 34.412$; $n = 312$; $p < 0.01$). Most notably, males engaging in more costly alarm calls or counterattacks directed them far more often to predatory dogs (65% and 75%, respectively) than non-predatory ones, compared to males eliciting the less energetically costly flee and/or freeze response to predatory dogs (53%), which was nearly random. Only 3% (63/1971 responses) of the time did an adult male involved in an encounter give two different types of responses. Responses were highly consistent within males, suggesting that males exhibiting the least costly flee and/or freeze responses may not have recognized the difference between predatory and non-predatory dogs or were indifferent.

All successful predatory attacks by dogs that we observed took place in the agricultural field where langurs are vulnerable due to the absence of connected tree cover, affording a low probability of escape (see Supplementary Video 5). Sub-adults were the most likely to be killed, perhaps because they tended to feed away from adult males, making it difficult for adult males to immediately rescue them or chase the dogs away in time (Table 2). Adult males were always close to infants/juveniles and their mothers when the group fed in the agricultural fields. Although infants and juveniles were most frequently injured by the dogs, such attacks did not result in fatalities because adult males could quickly intervene either by directly attacking the dog or giving alarm calls.

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

Observation 1, the rescue of the infant by adult males: August 3, 2018, between 0950 and 1005 h

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 troop. An infant (4 months old) is playing up in a small tree next to the big oak tree where all individuals

Fig. 1 Dog–langur encounters. Sub-adult langurs were killed (**a**) and consumed (**c**) by dogs. Adult male and dog fighting (**b**, **d**)

are resting. At 0950 hours, the infant falls 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 picks him up and again shakes him violently. Many langurs now rush to the scene and start aggressively grunting at the dogs. At 0952 hours Maya and Bhuru move about 5 m away from the langurs; Bhuru continues shaking the infant in his mouth. Adult male langurs, Hari and Remo chase after the two dogs. Bhuru drops the infant, and it is immediately picked up by the mother, who carries it back to the big oak tree. Hari and Remo chased both dogs away from the oak forest. It did not seem possible that the infant would survive, but it remained conscious and was able to hold onto its mother. The infant recovered and was alive throughout the remainder of this study.

Observation 2, the rescue of a juvenile by adult males: 17 May 2017: between 1150 and 1216 h

At 1150 hours the langur group enters the agricultural fields located very close to Siroli village. At 1153 hours the group is spotted by village dogs. At 1155 hours, three 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 Thelka tree (*Ficus neriifolia*) 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, the juvenile is effectively trapped in the small fig tree. All three dogs remain under the fig tree. At 1159 hours, the juvenile emits loud alarm calls in the direction of the cliffs approximately 600 m from the fig tree. At 1206 hours 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 1209 hours, Remo runs toward the dogs and distracts them from the trapped juvenile, enticing the dogs to chase after him and engage in fighting. At 1210 hours, Hari approaches the lone dog remaining under the fig tree, still barking at the juvenile. Hari distracts the attention of this dog. At 1212 hours, 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 m 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 to the cliffs. At 1216 hours, the juvenile safely rejoins the group.

Attributes of adult males displaying antipredator behaviors

Nine adult males performed anti-predator behaviors; the details of five predictor variables corresponding to each adult male are shown in Table 4. In total, 749 copulations and 3032 grooming bouts were recorded (a total of 326 h) between the nine adult males and 32 adult females.

Residency duration and rank

Adult males Hari and Remo had the longest period of residency (1672 days), being present in the troop since the study began. Orange and Thumri had the shortest residency, 92 days. The other adult males entered the troop during the start of the mating season between May and August of 2016, 2017, or 2018. Troop residency tended to be negatively correlated with rank, but this relationship was not statistically significant ($r_s = -2.79$, $p = 0.469$, $n = 9$). While some males entered the troop and quickly became alpha (i.e., Julio, Viru, and Thumri), others came in and remained at low-ranking positions (i.e., Muki and Orange) (Table 4).

Genetic relatedness

Figure 2 presents the genetic structure of the study group based on cladistic analysis of mtDNA sequences. We found high genetic diversity among the adult males, represented by seven different mitochondrial DNA haplotypes (Supplementary Material 3, Fig. 2). Three males (Remo, Viru, and Thumri) belonged to haplotypes 1, 2, and 3, respectively. These were the only haplotypes associated with adult females in the group. It is possible that they left as immature males and returned as adults. This means that these males are maternal siblings and or cousins of females in the study group. The remaining males had haplotypes not recognized in any of the female group members currently present, making these males true non-kin of group members.

Grooming and mating rate

There was no relationship between rank and rates of grooming ($r_s = 0.2$, $p = 0.614$, $n = 9$). Longer resident males Hari and Remo received the most grooming and displayed the highest rates of antipredator behavior. Shorter resident and maternal sibling, Viru also received high rates of grooming, but did not perform a high rate of counterattacks or alarm calls (Table 4). High-ranking immigrant adult males had greater access to receptive females and consequently exhibited higher mating rates compared to lower-ranking adult males ($r_s = 0.767$, $p = 0.022$, $n = 9$).

Table 4 Adult male characteristics

Adult males	Total observation hours	Total number of dog encounters	mtDNA haplotype	First reported in troop	Residency duration (days)	Normalized David score (rank)	Mating rate/h	Grooming rate/h	% of antipredator behavior*		
									Counterattack	Alarm call	Flee-freeze
Gichu	269	298	Type 4	May, 2016	942	4.48	0.32	0.15	6.45	9.79	17.19
Hari	239	341	Type 4	June, 2014	1672	2.48	0.14	0.32	47.10	29.97	11.42
Julio	260	230	Type 4	August, 2017	457	5.89	0.56	0.15	3.87	3.67	14.24
Muki	252	155	Type 5	July, 2017	487	0.85	0.2	0.1	0.00	13.15	7.52
Nati	276	320	Type 4	May, 2016	942	3.18	0.57	0.13	7.10	5.81	19.48
Orange	109	99	Type 6	August, 2018	92	1.59	0.17	0.12	0.00	7.03	5.10
Remo	265	336	Type 2	June, 2014	1672	1.75	0.11	0.21	33.55	25.69	13.43
Thumri	119	100	Type 3	August, 2018	92	5.4	0.84	0.16	0.00	2.14	6.25
Viru	128	92	Type 1	July, 2018	122	6.66	1.1	0.13	1.94	2.75	5.37

*The percentage is calculated by dividing the total antipredator behavior responses of each male by the total antipredator behavior responses of all males

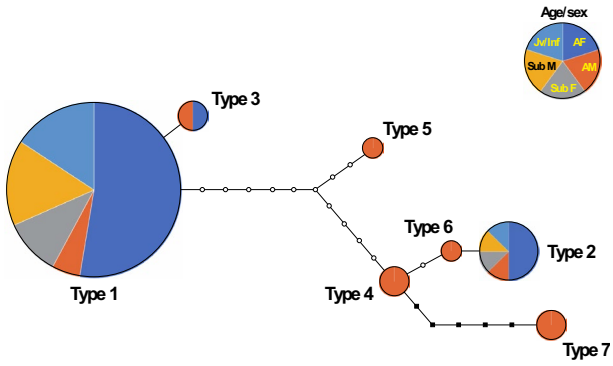

Fig. 2 Genetic structure of the study group of the Central Himalayan Langur (*Semnopithecus schistaceus*). MtDNA genealogy network was constructed by cladistic analysis based on the algorithm of Templeton et al. (1992) using the control region (1086 bp) data of 54 individuals (see Supplementary Material 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

Predictive factors of antipredator behavior

Among the eight models tested, the integrated model was the best-approximating model for explaining the benefit of anti-predator behavior. This model had the lowest AICc value and the highest model probability (i.e., weight = 1, Table 3), which include the variables residency duration, genetic relatedness, grooming rate, rank, and mating. The remaining seven models including the null model (Table 3) had a combined probability of less than 0.01.

The log odds of counterattack over flee and/or freeze responses by adult males with longer group residency was 0.002, whereas to give an alarm call it was 0.001 (Table 5). The longer-duration resident adult males gave more alarm calls and fought directly with dogs significantly more often compared to shorter-duration resident males (Table 5; $z = 3.939$; $p < 0.01$; $z = 5.675$; $p < 0.01$) (Fig. 3d). The interaction between adult male id and residency duration showed a significant positive association between the performance of counterattack over flee and/or freeze responses for the adult males Hari, Nati, Remo and Viru, and a negative association for adult males Gichu, Muki, Orange and Thumri. The interaction between adult male id and residency duration had a significant positive association between the performance of alarm call over flee and/or freeze response for the adult males Gichu, Hari, Muki and Remo (Table 6, Fig. 4a and b).

The log odds of performing a counterattack over flee and/or freeze by maternal siblings and/or male cousins was − 0.191, whereas for giving alarm calls it was − 0.322 (Table 5). Maternal siblings and/or cousins performed significantly lower rates of counterattacks than non-kin males

Table 5 Results from a multinomial logistic regression model with counterattack and alarm call as response variables

Model	Predictor variable	Counterattack			Alarm call		
		z value	*p* value	Coef (SE)	*z* value	*p* value	Coef (SE)
Integrated	Residency duration	5.675	**< 0.01**	0.002 (0.0003)	3.939	**< 0.01**	0.001 (0.0003)
	Genetic relatedness	− 1.794	**< 0.01**	− 0.191 (0.050)	− 1.154	0.527	− 0.322 (0.040)
	Grooming rate	2.205	**< 0.01**	1.754 (0.031)	3.780	**< 0.01**	0.275 (0.031)
	Rank	− 2.603	**< 0.01**	− 0.589 (0.125)	− 4.099	**< 0.01**	− 0.436 (0.126)
	Mating rate	− 0.302	0.763	0.182 (0.162)	− 1.839	**< 0.01**	− 0.322 (0.070)

Coef (SE) Log odd coefficient (standard error)

Bold values represent the significant level

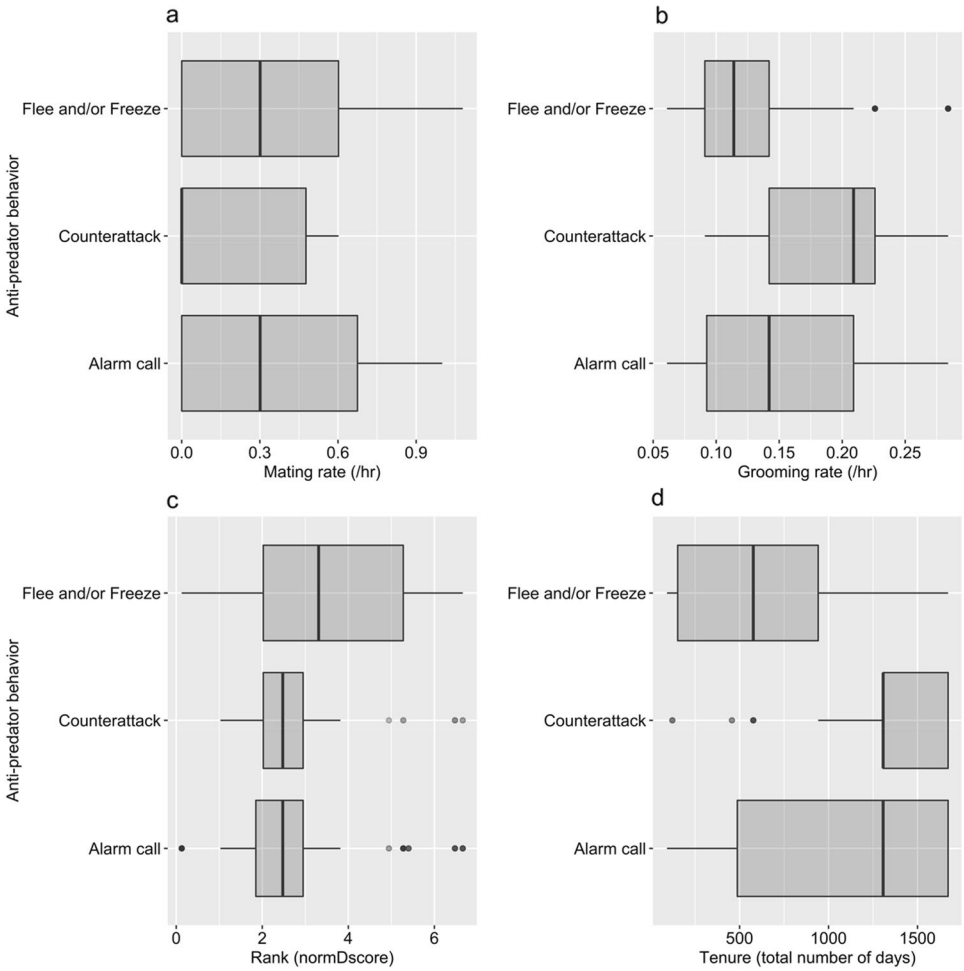

Fig. 3 Predictor variables in relation to anti-predatory response by adult males ($n = 312$). The box bound the Interquartile range (difference between the upper and lower quartiles) divided by the median while the whiskers extend to a maximum of 1.5 × Interquartile range beyond the box

(Table 5; $z = -1.794$; $p < 0.01$). The interaction between adult male id and genetic relatedness displayed a significant positive association between the performance of counterattack over flee and/or freeze responses for adult male Remo, and a negative association for adult males Thumri and Viru. The interaction between adult male id and genetic relatedness displayed a significant positive association between the selection of alarm call over flee and/or freeze for the adult male Remo (Table 6, Fig. 4).

The log odds of performing a counterattack over a flee and/or freeze response by adult males with higher grooming rates was 1.754, whereas for alarm calls it was 0.275 (Table 5). Adult males who received high rates of grooming from females also performed high rates of counterattack and alarm call, compared to males who received low rates

Table 6 Results of multinomial logistic regression models for all adult male interactions with predictor variables

Predictor variable	Counterattack		Alarm call	
	p value	Coef (SE)	*p* value	Coef (SE)
Residency duration*Idg	**< 0.1**	− 0.003 (0.001)	**< 0.1**	0.003 (0.001)
Residency duration*Idj	0.508	0.002 (0.003)	0.138	0.004 (0.001)
Residency duration*Idm	**< 0.01**	− 0.106 (0.001)	**< 0.01**	0.004 (0.001)
Residency duration*Idn	**< 0.01**	0.002 (0.005)	0.456	− 0.002 (0.001)
Residency duration*Ido	**< 0.01**	− 0.337 (0.001)	0.895	0.005 (0.004)
Residency duration*Idr	**< 0.01**	0.002 (0.002)	**< 0.01**	0.004 (0.001)
Residency duration*Idt	**< 0.01**	− 0.275 (0.001)	0.216	0.011 (0.008)
Residency duration*Idv	**< 0.01**	0.025 (0.008)	0.112	0.012 (0.008)
Genetic relatedness*Idr	**< 0.01**	0.188 (0.040)	**< 0.01**	0.322 (0.050)
Genetic relatedness*Idt	**< 0.01**	− 0.003 (0.001)	0.216	0.001 (0.001)
Genetic relatedness*Idv	**< 0.01**	− 0.002 (0.001)	0.112	0.001 (0.001)
Grooming rate*Idg	**< 0.01**	− 0.063 (0.001)	**< 0.01**	− 0.047 (0.008)
Grooming rate*Idj	0.662	0.003 (0.007)	0.262	− 0.009 (0.008)
Grooming rate*Idm	**< 0.01**	− 0.439 (0.001)	**< 0.01**	− 0.066 (0.012)
Grooming rate*Idn	**< 0.01**	− 0.021 (0.001)	**< 0.05**	− 0.013 (0.006)
Grooming rate*Ido	**< 0.01**	− 0.002 (0.001)	0.896	0.001 (0.001)
Grooming rate*Idr	**< 0.01**	0.099 (0.021)	**< 0.01**	0.170 (0.026)
Grooming rate*Idt	**< 0.01**	0.003 (0.001)	0.216	0.001 (0.001)
Grooming rate*Idv	**< 0.01**	− 0.002 (0.001)	0.112	0.001 (0.001)
Rank*Idg	**< 0.01**	0.533 (0.008)	**< 0.01**	− 0.395 (0.071)
Rank*Idj	0.662	0.067 (0.154)	0.262	− 0.206 (0.183)
Rank*Idm	**< 0.01**	3.991(0.001)	**< 0.01**	0.601 (0.105)
Rank*Idn	**< 0.01**	− 0.668 (0.019)	**< 0.05**	− 0.417 (0.201)
Rank*Ido	**< 0.01**	− 0.006 (0.001)	0.895	0.001 (0.001)
Rank*Idr	**< 0.01**	0.783 (0.168)	**< 0.01**	1.339 (0.208)
Rank*Idt	**< 0.01**	− 0.016 (0.001)	0.216	0.001 (0.001)
Rank*Idv	**< 0.01**	0.001 (0.004)	0.112	0.001 (0.004)
Mating rate*Idg	**< 0.01**	− 0.006 (0.001)	**< 0.05**	0.325 (0.197)
Mating rate*Idj	0.96	0.012 (0.244)	0.316	0.240 (0.239)
Mating rate*Idm	**< 0.01**	− 2.192 (0.001)	**< 0.01**	0.656 (0.142)
Mating rate*Idn	**< 0.01**	− 0.516 (0.120)	**< 0.01**	0.603 (0.112)
Mating rate*Ido	**< 0.01**	1.641 (0.001)	**< 0.05**	0.472 (0.234)
Mating rate*Idr	0.349	0.116 (0.124)	**< 0.01**	0.880 (0.253)
Mating rate*Idt	**< 0.01**	− 0.380 (0.001)	**< 0.01**	− 0.662 (0.001)
Mating rate*Idv	**< 0.01**	− 0.164 (0.001)	**< 0.01**	0.409 (0.001)

An asterisk * refers to an interaction term. All comparisons were made against the adult male Hari

Coef (SE) Log odd coefficient (standard error), *Id* adult male id, *g* Gichu, *j* Julio, *m* Muki, *n* Nati, *o* orange, *r* Remo, *t* Thumri, *v* Viru

Bold values represent the significant level

of grooming (Table 5; $z = 2.205$; $p < 0.01$ Table5; $z = 3.780$; $p < 0.01$ (Fig. 3b). The interaction between adult male id and grooming rate showed a significant positive association between the performance of counterattack over flee and/or freeze responses for adult males Hari, Remo and Thumri, and a negative association for the adult males Gichu, Muki, Nati, Orange and Viru. The interaction between adult male id and grooming rate showed a significant positive association between performance of alarm call over flee and/or freeze responses for the adult males Remo and Hari, and a negative association for the adult males Gichu, Muki and Nati (Table 6, Fig. 4e and f).

The log odds of performing a counterattack over flee and/or freeze responses by high-ranking males was − 0.589, whereas the log odds for giving alarm calls was − 0.436 (Table 5). Low-ranking males performed significantly more alarm calls and fought more with dogs compared to high-ranking males (Table 5; $z = -2.603$; $p < 0.01$; $z = -4.099$;

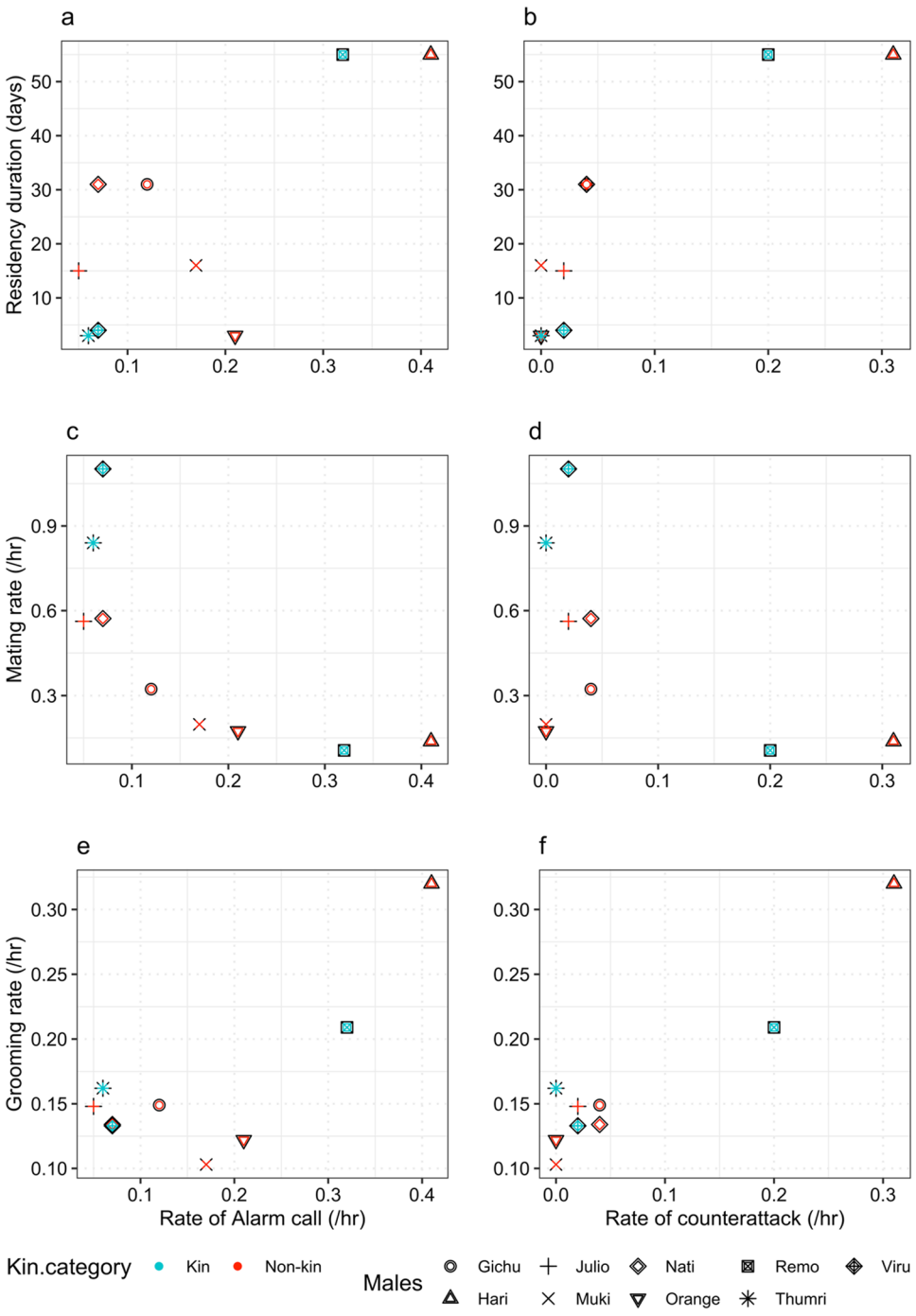

Fig. 4 Predictor variables in relation to emitting alarm calls and engaging in counterattacks by each adult male ($n = 9$ adult males)

$p < 0.01$) (Fig. 3c). The interaction between adult male id and rank showed a significant positive association between the performance of counterattack over flee and/or freeze responses for the adult males Gichu, Muki, Hari, Remo and Viru, and a negative association for the adult males Nati, Orange and Thumri. The interaction between adult male id and rank showed a significant positive association between the performance of alarm call over flee and/or freeze responses for the adult males Hari, Muki and Remo, and a negative association for the adult males Gichu, and Nati (Table 6, Fig. 4).

The log odds of performing alarm call over flee and/or freeze responses by adult males with higher mating rates was − 0.322 (Table 5). Adult males who had high rates of mating performed significantly lower rates of alarm calls than males who had low rates of mating (Table 5; $z = -1.839$; $p < 0.01$) (Fig. 3b). The interaction between adult male id and mating rate showed a significant positive association

between the performance of counterattack over flee and/or freeze responses for the adult male Orange, and a negative association for the adult males Gichu, Muki, Nati, Thumri and Viru. The interaction between adult male id and mating rate showed a significant positive association between the performance of alarm call over flee and/or freeze responses for the adult males Gichu, Muki, Nati, Orange, Remo and Viru, and a negative association for the adult male Thumri (Table 6).

Discussion

Males play a special role in group predator defense (Arlet and Isbell 2009; Dolotovskaya et al. 2019), and primate groups under high predation pressure tend to contain more males, arguably because they are needed to protect females and younger group members against predators (Cheney and Wrangham 1987; van Schaik and Hörstermann 1994). However, it is not known if all males within the same group contribute equally or exhibit similar types of antipredator behavior. This study investigated the behavioral strategies of adult male CHL in response to serious dog predation pressure in a human-dominated landscape. We investigated four hypotheses for the benefit of anti-predator behavior using a dog–langur predation encounter model. This study pursued an information theory approach to examine multiple hypotheses simultaneously and objectively. By doing so, we showed that the benefit of anti-predator behavior by CHL adult males is better explained by an integrated model including the variables residency duration (parental care hypothesis), genetic relatedness (kin selection hypothesis), grooming rate (reciprocal altruism hypothesis), rank, and mating rate (costly signaling hypothesis).

Our results showed that not all males contributed to predator defense equally. In short, we found that counterattacking behavior was most clearly linked to males that have lived in the group for longer periods of time, that have better established social (grooming) relations with females in the group and/or who are related to them through maternal sibling and or cousin ties. While not verified, it is also possible that some potentially have offspring with females in the group whom they are protecting. Mutually nonexclusive in some instances, these patterns are most consistent with the parental care hypothesis and the kin selection hypothesis. In contrast, newly immigrant high and low ranking males exhibited less costly antipredator behaviors, had no maternally kin-related females in the group, and were not likely to yet have offspring in the group. Freeze and/or flee, exhibited mostly by high-ranking newly immigrant males is more about self-preservation than group protection. Low-ranking individuals with lower mating rates, but higher rates of alarm call behavior, do so perhaps to advertise their quality as a mate, which is consistent with the costly signaling hypothesis. Adult males with shared interests (long-tenured males) are may be working together, while newer males are basically looking out for themselves, perhaps until they have social and offspring interests in the group to defend. We further break down these points below.

Parental care and risks taken by adult males

Male parental care in primates is generally indirect, such as protecting the young from predators. Two natal and long-term resident adult males, Hari and Remo, in the study group showed high rates of direct fighting with dogs, while other males did not. Interestingly, when the study began, Hari was the alpha male. Given the characteristically high mating frequency of alpha males, it is possible that Hari indeed had several offspring in the group during the study. It has been suggested that such males have sired offspring in the group and are protecting their earlier reproductive investments (Smuts 2017). Therefore, protection of offspring might be an anti-predation tactic for only the longest resident males (also see below for putative kin). This may explain why Hari and Remo protected the group members against predators more than recent immigrant males. A similar trend was observed in gray-cheeked mangabeys (*Lophocebus albigena*), where high-ranking adult males, who possibly have more offspring in the group (Arlet et al. 2007), engaged more in active defense against predatory African crowned eagles (Arlet and Isbell 2009).

Protection of putative kin

Protection of kin as a tactic is confirmed in various mammals, like Belding's ground squirrel (*Spermophilus beldingi*) (Sherman 1977), the chipmunk (*Eutamias sonamae*) (Dunford 1977), and primates, e.g., vervet monkeys (*Chlorocebus pygerythrus*) (Cheney and Seyfarth 1985), where the likelihood of giving alarm calls is affected by kinship. We found that protection of kin as a tactic is not the only reason for performing counterattacks and alarm calls by the adult males Remo, Thumri and Viru, who shared the same mtDNA haplotype with group females. Male tactics appear to be more nuanced, based on multiple attributes. Thumri and Viru, short-term resident males who were re-entering into the natal group performed counterattacks less frequently than long-term resident male Remo. However, for a better understanding of the kin selection hypothesis we need more observations from related adult males. Our data examined kinship associated with maternal siblings and/or cousins (non-descendant kin), but the protection of offspring (direct descendent kin) by adult males is explained by the parental care hypothesis. For understanding the role of kin selection in CHL antipredator behavior, it is important to determine

whether males are protecting their siblings/cousins, or if they are protecting their offspring. This can be further elucidated in the future with more long-term antipredator behavior data on both resident and immigrant maternal siblings.

Exchange of grooming for support

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. Specifically, individuals that groomed more also supported each other more during agonistic encounters. In this study, it was shown that males who received more grooming from female partners are associated with high and/or intermediate antipredator behavior. This association could be beneficial for the females and their vulnerable offspring. Hari and Remo were both resident males who performed the highest rates of counterattacking and received the highest rate of grooming from females than other adult males, even though they were low in social rank and had lower mating rates. This suggests that females may have a social preference for protective males, but even so, the benefits for such males in maintaining such bonds remain unclear, at least from the perspective of mating benefits. One possible explanation could be a female strategy to maintain close bonds with males who protect them and their offspring but to mate with the novel incoming males. This is consistent with the evolution of adult female behavioral strategies for forming social relationships in terms of inclusive fitness (direct reproductive value plus the reproductive value of one's relatives) (Wrangham 1980).

For the resident adult males, risk of moving to another group and not being able to enter at the top is likely to be high. Therefore, 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 a host's fitness (Lehmann 1993).

Mating benefits were not linked to costly signaling

We found that low ranking, recently immigrated males perform high rates of costly alarm calls, that could bring attention to themselves. Such males did not have offspring, siblings, or social partners in the group, nor did they have high mating success. Such behavior may best be interpreted as a way of advertising their mating and parenting quality. This is similar with other studies suggesting that lower ranking males with fewer mating opportunities (Launhardt et al. 2001) emit costly signals as an alternative male reproductive tactic (van Schaik et al. 2021). In CHL reproductive success and rank depend on troop takeover during the mating season (Borries 2000; Borries et al. 2017) Top-ranking adult male Julio entered the group in August 2017 and quickly took over as alpha male. Likewise, in July 2018, Viru entered the group and took over as the new alpha. The three highest-ranking males at the time (Viru, Julio, and Thumri) achieved the highest mating success of all males but engaged minimally in high (counterattack) and intermediate cost (alarm calls) anti-predator behaviors. Because high-rank males rarely engage in costly anti-predatory behavior, the potential for such males to display counterattacks to demonstrate their ability as potential mate is a less likely explanation for the function of this behavior in CHL.

Learning anti-predator behaviors

While we did not set out to address the role of social or individual learning in the performance of antipredator behaviors, our observations uncovered a possible link, which we briefly discuss here. In some animal species, anti-predatory alarm calls in response to predators in the environment are considered to be a learned behavior (vervets *Chlorocebus pygerythrus*, Seyfarth and Cheney 1980; rhesus, Mineka et al. 1980). In dwarf mongoose (*Helogale undulata*), such anti-predator behaviors are transmitted from older siblings to younger ones (Rasa 1987). Himalayan wolves (*Canis lupus chanco*) are found widely across the Himalayan and Trans-Himalayan landscape of India (Habib et al. 2013), which is also the distribution range of Himalayan langurs. Since domestic dogs are descended from the grey wolf (*Canis lupus*) (Frantz et al. 2016), adult males may derive part of their anti-predator tactics from that which evolved from their interactions with wolves over their evolutionary history. However, we found that males with greater potential exposure to domestic dogs over time (longer tenured) in the group behaved more aggressively toward individuals with predatory tendencies than those without. Hari and Remo displayed a greater awareness of the village dogs' predatory behavior, and this was shown by their seemingly greater confidence to act aggressively and come to the aid of vulnerable group members. These two males performed all of the observed successful rescues.

While our observations cannot squarely address whether counterattacking behavior is learned or not, we suggest that predatory dogs could be quite intimidating to males with little previous experience with them. Counterattacks

are energetically more costly, so newly immigrated adult males may also be less prepared to face attacks if they are not familiar with each dog's different predatory tendencies toward langurs. Four other CHL groups observed in forests at higher altitudes in the area where dogs were not always present have other predators to contend with (leopards, Ross 1993; bears, Bishop 1975; hawks and eagles), each having entirely different kinds of predatory behaviors than dogs. Different anti-predatory behaviors might be learned by different groups according to differing predator compositions and threats. Future work focusing on the anti-predatory behavior towards these different species may shed further light on the question of learning predator-defense behaviors by CHL.

Crop foraging as risky behavior

Primates in many places are reported to adjust their behavior in response to the risks of foraging in agriculture fields (Smith et al. 2008; Link and Di Fiore 2013; Lindshield et al. 2017). This can be done by reducing the rate of vocalizations (Wilson et al. 2007), increased group cohesiveness and vigilance (Hockings et al. 2012), and crop foraging at night (Krief et al. 2014). Feeding inside the agricultural field is risky behavior for langurs due to predatory encounters with domestic dogs. The CHL's home range in this study significantly overlaps with human-dominated landscapes, and they feed on the leaves of fodder crops growing at the edge of the terraced agricultural fields throughout the entire year, as well as in season crops for human consumption (Nautiyal et al. 2020).

The decision to forage in risky habitats is often a response to seasonal food shortages or rapid habitat degradation (Hill 2018; McLennan 2013). The consequences of such a decision however incur costs that can lead to increased risk of injury or even death (Hill 2017; this study). When there is a positive correlation between food abundance and predation risk, adult males undertake high-risk foraging while females tend to sacrifice such risky foraging benefits to minimize predation risk and enhance their fitness by minimizing risks to their offspring (Sukumar 1991; Bleich et al. 1997; Hay et al. 2008). However, CHL of all age–sex classes foraged inside the fields. This was possible because some adult males were able to perform effectively antipredator behavior against dogs to cope with the risk associated to the most vulnerable females and their offspring during predatory encounters. This behavioral strategy was essential for langurs of our study group to be able to enter effectively and utilize the resource inside critical part of their home range. In locations where langurs and humans live sympatrically, a better understanding of such risk-taking behavior might provide important insights for understanding and mitigating the problem of crop feeding (Nautiyal et al. 2020).

Anti-predatory behavior display by adult male langurs is energetically costly and entails risks. While injury or death to adult males from encounters with dogs were not observed during the study, the injury or death of four adult male langurs was recorded elsewhere in the study area. In A group, sharing a boundary with S group, an unidentified adult male was killed and consumed by a dog in the Sanso village (Supplementary Video 6). Up in the high-altitude meadows (3500 to 4000 m), a group of three shepherd dogs was observed to kill two adult male langurs during counterattacks. This happened when the langurs were foraging out in the open meadows away from the safety of trees. In another instance, one solitary non-group adult male was killed by two dogs in S group's territory, who had been following S group from a distance for a couple of weeks. Local people reported to us that his death occurred inside the agricultural field. After our observations for this study were concluded, we received information from local assistants in the village that in March 2021, an adult male (assumed to be Remo) was also killed and eaten inside the agricultural fields.

Conclusions

This study provides insights into the behavioral flexibility of CHL and their high degree of behavioral adaptation to their environmental circumstances. Based on our results, we predict that under the social organization and mating system of CHL, as rank and tenure duration of adult males in the group changes, so too will their antipredator behavioral strategies. In particular, low-risk-taking, high-ranking males are likely to become more active in defense of the group as their investment in it increases with time. All group members are affected, as the cumulative impact of dog predation can have both a direct and indirect impact on the survival and growth of CHL populations over the long term. A better understanding of the effects of predation risk is crucial for primate conservation. Further systematic studies on dog-related antipredator behavior will help expand our understanding of the effects of human impacts on behavioral flexibility, predation risk, and their ability to survive in ever increasing human-modified environments. Planning for wildlife management and conservation will be better informed with a deeper understanding of dog-primate interactions. (Creel and Christianson 2008; Zanette et al. 2011).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-023-01061-0.

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Data availability All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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