Beyond group size effects: vigilance and social monitoring in Nepal gray langurs

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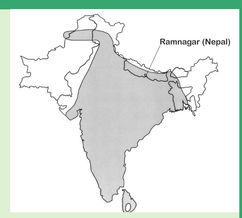
Introduction

- Vigilance, the monitoring of the surrounding environment, may serve different functions:
  - non-social vigilance (vigilance directed at targets not located within the individual's social group) may serve to detect threats from both predators (Caro 2005) and conspecifics (e.g. outside competitors: Cowlishaw 1998).
  - social monitoring within an individual's group can detect threats from group mates, e.g., food competition, mate competition, infanticide (Steenbeck et al. 1999; Treves 1999).
- Vigilance directed at predators should decrease with group size, because of 'dilution' and 'many eyes' effects (Pulliam 1973). This group size effect, though common in many species, is largely absent in primates (Treves 2000; Caro 2005; Allan and Hill 2018).
- The lack of a group size effect may be explained by:
  - not distinguishing between targets of vigilance; i.e., increased group size can increase pressures for social monitoring (Caro 2005), potentially masking decline in non-social vigilance.
  - greater biological relevance of perceived, rather than actual, group size and thus of the presence of individuals in proximity (Metcalfe 1984).
- Distinguishing between targets of vigilance and neighbor density may help to solve this issue.

Study Objective and Predictions

- We investigated the functions of non-social vigilance (NSV) and social monitoring (SM) in Nepal gray langurs (*Semnopithecus schistaceus*), predicting that:
  - NSV may serve antipredator and extra-group functions
  - SM may serve within-group functions
  - see Table 1 for specific predictions

Study Site and Study Species



- *Study site:* Ramnagar, Nepal (300 m a.s.l., 27°44'N, 84°27'E)
- *Population:* Langurs live in a range of group sizes displaying varied degrees of group spread (Koenig et al. 1998) and can have both multi- and unimale groups (Koenig and Borries 2001).
- *Mating seasonality:* conceptions occur from July to November (Borries et al. 2001)
- *Male immigration:* mainly during the mating season (Borries 2000)
- *Predation:* 21.4% of all adult females and immatures known to have died/disappeared due to predation (de Vries et al. 2016)
  - Possible predators: leopards and domestic dogs (confirmed), jackals, jungle and leopard cats, tigers, 4 species of birds of prey
- *Infanticide:* risk of infanticide amounting to about 1/3 of infant mortality (Borries and Koenig 2000)

Methods

- Focal instantaneous sampling data of NSV and SM collected in two groups of wild Nepal gray langurs (*Semnopithecus schistaceus*) from January 1994 to January 1995:
  - 30 s intervals over a half hour period each, i.e., 60 sample points (59,551 total)
  - Group A ('small group'): 1-3 adult males and 2-3 adult females (9-10 individuals total)
  - Group O ('big group'): 3-5 adult males, 14-15 adult females (26-34 individuals total)
- Proximity to group members (≤ 3 m) also recorded at sample point
  - Infant proximity: unweaned offspring ≤ 3 m to its mother
  - Group A: 2 infants and Group O: 10 infants
- Proportion NSV and SM out of total sample points arcsine transformed and analyzed using linear mixed effects models using 'lmer' function of 'lme4' package (Bates et al. 2015) in R v. 3.4.0 (R Core Team 2017)
- Fixed effects: Group membership, Proximity, Infant proximity, Sex (of focal), Mating season
- Random effects: Focal individual, Sampling Period, ID
- Proximity, Infant proximity, and Mating season analyzed via repeated measures LMEs to account for paired data (paired via random effect ID; Pairs: Yes and No)

Results

- Individuals (N = 27) non-socially vigilant for 24.0 ± 9.1% of sample points and socially monitoring for 4.6 ± 2.5%

Table 1. Predictions and *p*-value for associated model for antipredator, extragroup, and within-group vigilance. Proportion of non-social vigilance or social monitoring: ↑ = increase, ↓ = decrease. **Bolded** p-values indicate those < 0.05. [a] direction of effect contrary to prediction

Function of vigilance	Variable	Direction	Prediction	*P*-value
antipredator	group size	↓	non-social vigilance with group size	0.300
	sex	↑	male non-social vigilance than female	**0.002**
	proximity	↓	non-social vigilance in proximity	**< 0.001**
	infant proximity	↑	mother non-social vigilance in proximity to own infant	**< 0.001**
extra-group	mating season	↑	male non-social vigilance during mating season	**0.043**[a]
within-group	group size	↑	social monitoring with group size	**0.019**
	proximity	↑	social monitoring in proximity	0.560
	infant proximity	↑	mother social monitoring in proximity to offspring	**< 0.001**
	mating season	↑	male social monitoring during mating season	**< 0.001**

Anti-predator function

- NSV declined with proximity, but not with group size (Table1, Fig. 1).
- Males displayed more NSV than females (Table 1).
- Mothers displayed more NSV when in proximity to their infants (Table 1).

Extra-group function

- Males showed less NSV during the mating season (Table 1).

Within-group function

- SM increased with group size, but not proximity (Table 1, Fig. 1).
- Mothers displayed more SM when in proximity to their infants (Table 1).

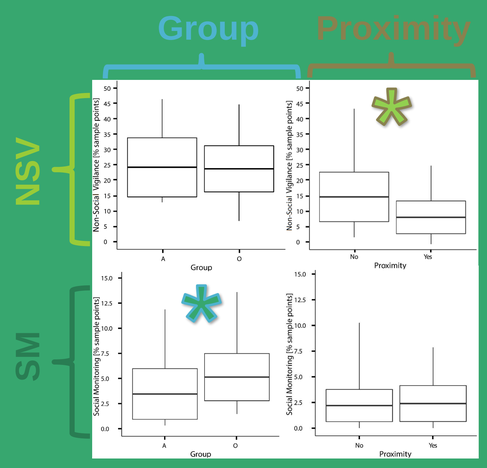


Figure 1. Percentage of non-social vigilance and social monitoring by group size and proximity status. Dark line indicates means. Boxes represent standard error and whiskers standard deviation. For group size: Group A: 7 adult individuals, Group O: 20 adult individuals; *N* = 107 data points. For proximity: graph represents averages for proximity categories independently. Statistical tests were performed with paired data per focal animal and observation period; *N* = 107 data pairs (27 individuals). Asterix represents significant difference in vigilance type across categories (*P* < 0.05).

Summary and Conclusions

- We found evidence for antipredator, but not extragroup, functions of non-social vigilance (NSV) and within-group functions of social monitoring (SM) in Nepal gray langurs.
- Group size and proximity exhibited contrasting effects for NSV and SM:
  - A proximity effect for NSV suggests that neighbor density is a more important factor in perceived predation risk than overall group size (Metcalfe 1984). The general use of group size instead of neighbor density might explain the absence of a group size effect among primates (Caro 2005).
  - A group size effect for SM could indicate increased mating competition (males) or feeding competition (females) or both with larger groups
  - The lack of a proximity effect for SM may be due to unexplored factors including position within the group (Gaynor and Cords 2012) or having 'trusted neighbors' (Fraser et al. 2008).
- Males displayed higher NSV than females:
  - Males may provide a service to mates and potential offspring (Baldellou and Henzi 1992).
  - Male NSV could also serve the dual function of being vigilant for both predators and extragroup competitors (Caro 2005).
  - An increased need to monitor within-group competitors and receptive females during the mating season may lead to a trade-off between NSV and SM (Treves 2000).
- Females displayed both higher NSV and SM when dependent offspring were in proximity
  - Threat of predation and of infanticide may require both high NSV and SM, indicating a form of maternal care.
- The multifunctionality of vigilance makes it imperative to distinguish its targets and to consider a range of confounding factors when testing driving forces behind vigilant behaviors (Caro 2005)

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