Japanese macaques relax vigilance when surrounded by kin

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Abstract

Vigilance behaviour in group-living animals helps to detect threats. Individual vigilance levels are thought to decrease as group size or the number of neighbours increases. However, the results of studies on the effects of group size or the number of neighbours are inconsistent, especially in primates. Since social vigilance (i.e. monitoring for group members) plays an essential role in group-living primates, discrepancies among studies may have been caused by differences in the quality of social relationships between group members. Using data from a provisioned group of Japanese macaques, *Macaca fuscata*, this study examined the effects of the quality of social relationships and the number of neighbours on vigilance levels. We found that the frequency of vigilance was lower when the majority of an individual's neighbours were kin than when kin were in the minority. Since Japanese macaques show strong nepotism and cope with social threats by forming coalitions between close kin, individuals may be able to reduce their vigilance levels by relying on the vigilance of potential allies. Furthermore, when the majority of neighbours were kin, the proportion of time spent on vigilance decreased as the number of neighbours increased. However, when kin were in the minority of neighbours, the number of neighbours did not affect vigilance levels. Overall, our results indicate that the quality of social relationships with neighbours and the number of neighbours interactively affect vigilance levels.

Keywords

Japanese macaque, *Macaca fuscata*, relationship quality, social monitoring, vigilance

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Vigilance behaviour in group-living animals serves to detect and monitor surrounding threats, such as predators or conspecifics (Ebensperger, Hurtado, & Ramos-Jiliberto, 2006; Favreau, Goldizen, & Pays, 2010; Gaynor & Cords, 2012). In many species that use vigilance to detect predators, individual vigilance levels are negatively correlated with group size (i.e. the many-eyes effect; e.g. Lima, 1995; Clutton-Brock et al., 1999). Because individuals in a large group can rely on monitoring by others in the group, they can reduce their vigilance more than those in a small group (Pulliam, 1973). Other studies have shown that individual vigilance levels decrease with increasing numbers of nearby conspecifics, suggesting that animals share vigilance with nearby individuals rather than with all group members (Zhao, Lyu, Sun, & Zhou, 2019).

Reported effects of group size and the number of nearby conspecifics have not been consistent for primate vigilance (Allan & Hill, 2018). One reason for this may be that social vigilance (i.e. monitoring for group members) and antipredator vigilance are affected differently by group size or the number of neighbours (Treves, 2000). As several researchers have suggested, monitoring for conspecifics may serve an important function for group living, especially in primates (Chance, 1967; McNelis & Boatright-Horowitz, 1998; Tomasello, Call, & Hare, 1998; Treves, 2000). Since intragroup competition increases with group size and local density of competitors (van Schaik, 1983; Isbell, 1991; Wheeler, Scarry, & Koenig, 2013; Roberts & Cords, 2013), the need to monitor other individuals may increase as the group size or the number of neighbours increases. Hence, social vigilance is expected to increase as group size or the number of neighbours increases, in contrast to antipredator vigilance. Indeed, a positive relationship between group size or the number of neighbours and vigilance levels has been reported in brown capuchin monkeys, *Cebus apella* (Hirsch, 2002), chimpanzees, *Pan troglodytes* (Kutsukake 2006, 2007) and common marmosets, *Callithrix jacchus* (Gosselin-ildari & Koenig, 2012). Given that primates live in societies with highly structured social networks (Kudo & Dunbar, 2001; Silk, 2002; Kasper & Voelkl, 2009; Mac Carron & Dunbar, 2016), the presence, number or quality of social relationships with nearby group members may influence vigilance levels of individuals. For example, in some primate species, vigilance has been shown to increase when nonaffiliated individuals are nearby (mountain gorillas, *Gorilla beringei beringei*: Watts, 1998; chimpanzees: Kutsukake, 2006; brown capuchin monkeys: Pannozzo, Phillips, Haas, & Mintz, 2007). In addition, it has been reported that vigilance levels are reduced in the presence of close kin or individuals with a highly secure relationship (blue monkeys, *Cercopithecus mitis*: Gaynor & Cords, 2012; Geoffroy's spider monkeys, *Ateles geoffroyi*: Busia, Schaffner, & Aureli, 2019). However, little is known about how the effect of the number of neighbours on individual vigilance level is modulated by the quality of social relationships with neighbours. Therefore, this study used vigilance data from a provisioned group of Japanese macaques, *Macaca fuscata*, to examine how individual vigilance levels and the effect of the number of neighbours vary with the quality of social relationships.

Japanese macaques provide a valuable model to address these questions for several reasons. Despite having been studied for a long time, reports of predation on Japanese macaques are scarce (Takahashi,1997; Takahata, Huffman, Suzuki, Koyama, & Yamagiwa, 1999; Enari, 2014; but see Iida, 1999), suggesting that they experience little to no predation pressure. Although it is difficult to know the target of a gaze in a natural environment (Emery, 2000; Watson et al., 2015), vigilance in Japanese macaques is likely to be used primarily for monitoring group members (Kazahari & Agetsuma, 2010; Suzuki & Sugiura, 2011) and presumably other groups. Furthermore, Japanese macaque society is highly despotic (Thierry, 2000). In species with a despotic society and intense intragroup competition, social vigilance is likely to be more important than in other species (e.g. squirrel monkeys, *Saimiri sciureus*: Caine & Marra, 1988; yellow baboons, *Papio cynocephalus*: Alberts, 1994). Additionally, Japanese macaque society is characterized by strong nepotism and, therefore, there are strong social bonds between close kin (Chapais, Gauthier, Prud'homme, & Vasey, 1997). Matrilineal dominance rank is passed from mothers to their offspring (Chapais,1988; Kutsukake, 2000), and Japanese macaques respond to social threats by forming coalitions between close kin (Chapais et al., 1997). When mature kin,

which are closely affiliated and potential allies, are nearby, Japanese macaques may reduce their vigilance levels. Together with the aforementioned points, focusing on Japanese macaques allowed us to examine the impact of relationship quality on social vigilance rather than antipredator vigilance.

In this study, we tested several predictions. We distinguished the composition of neighbours of an individual as follows: if there were more mature kin than mature nonkin, we regarded the composition of neighbours as kin-majority. If there were fewer mature kin than mature nonkin, we regarded the composition of neighbours as kin-minority. We also regarded the composition of neighbours as kin-minority when the numbers of mature kin and nonkin were equal because our objective was to compare cases in which the number of mature kin was obviously larger than that of mature nonkin with cases in which it was not. As noted above, in Japanese macaques, mature kin can be potential allies in aggressive interactions (Chapais et al., 1997). Therefore, in situations where an individual is surrounded by kin-majority neighbours and thus has potential allies, the relative risk of social threats such as within-group aggression might be lower than in situations where an individual has few potential allies. Thus, we predicted that individuals would have lower vigilance levels when surrounded by kin-majority neighbours than when surrounded by kin-minority neighbours (Prediction 1).

We also investigated how the composition of neighbours moderates the effect of the number of neighbours on vigilance levels. Individuals that are surrounded by kin-majority neighbours would be able to depend on the latter's vigilance. Hence, we predicted that the more neighbours an individual had, the lower its level of vigilance would be. Conversely, when surrounded by kin-minority neighbours, vigilance level would not decrease as the number of neighbours increases (Prediction 2).

Because Japanese macaque society is extremely despotic, aggression is almost always directed from higher- to lower-ranking individuals (Thierry, 2000). Hence, the lower an individual's ranking, the more threats there are around the individual. Therefore, we predicted that the vigilance level of individuals with lower absolute dominance ranks would be higher than that of individuals with higher absolute dominance ranks (Prediction 3). Furthermore, vigilance levels would be higher when higher-ranked individuals were nearby than when they were not (Prediction 4).

Methods

Study Sites and Subjects

This research was conducted at Jigokudani Monkey Park in Shiga-Heights, Nagano Prefecture, Japan. S.I. conducted behavioural observations during July–October 2018 and July–September 2019. The total observation time was approximately 1008 h. The study group was a provisioned group of free-ranging Japanese macaques. Demographic records, including information on maternal kinship, of the group have been kept by the park staff since 1962. Because mature male Japanese macaques move between groups and some individuals are on the periphery of the group, it was not possible for us to determine accurately the number of individuals in the group; however, the group comprised approximately 240 individuals. In September 2019, there were 82 adult females (> 4 years of age), approximately 20 adult males (> 4 years of age), 110 juveniles (1–4 years of age) and 32 infants (< 1 year of age). We labelled both juveniles and infants as ‘immature’. The group was fed barley, soybeans and apples four times daily (0900, 1200, 1500 and 1630) by the park staff. Only the study group visited the park regularly, whereas other groups rarely approached the park.

Data Collection

To collect vigilance data, S.I. established a regular hexagonal patch (length of each side: 2 m) within the park area (Iki & Kutsukake, 2021). At the 0900, 1200 and 1500 feeding times, the

observer evenly distributed a total of 175 g of barley at seven locations inside the patch. No food was placed within 5 m of the patch. We used two digital video cameras (HDR-TD10 and HDR-PJ40V; Sony Corporation, Tokyo, Japan) at different angles to record for 15 min the vigilance behaviour of individuals that entered the patch, sat down at one of the seven locations and foraged. No intrusion by nongroup members was observed.

We estimated the dominance ranks of members of the subject group by observing unidirectional agonistic interactions between mature individuals using ad libitum sampling methods. We considered a unidirectional agonistic interaction to have occurred when individual A approached individual B, and B expressed submissive behaviour (e.g. a bared-teeth display) or fled, or when A unilaterally attacked B. Because maternal dominance rank is passed from mother to offspring in the Japanese macaque (Chapais, 1988; Kutsukake, 2000), we considered immature individuals to have the same rank as their mothers. We never observed a case of a mature male being defeated by a female in an agonistic interaction. Owing to the small number of mature males in our data set (N = 3 and 4 in 2018 and 2019, respectively) and the lack of cases of multiple males foraging in the patch, we assigned all mature males the highest rank (i.e. rank = 0). The dominance relationship was determined for all mature females.

Video Coding

We conducted video analyses using behavioural observation research interactive software (BORIS; Friard & Gamba, 2016). We recorded the name, age, sex, rank and kinship of all individuals that foraged in the patch. We considered each experimental session to consist of several phases during which group composition in the patch and individuals' positions remained unchanged. If an individual changed its position or moved out of the patch, or new individuals joined the patch to forage, we regarded this as the beginning of a new phase. All phases that lasted < 30 s were discarded from the analyses. Every phase during which fewer than two individuals were foraging in the patch (i.e. cases in which there were no neighbours) was also discarded. We defined the onset and offset of an individual's vigilance behaviour as when the individual raised his or her head and when the individual lowered his or her head, respectively (Bekoff, 1995; McDougall & Ruckstuhl, 2018). The onset and offset of vigilance were coded on a frame-by-frame basis (30 fps).

Overall, the data set consisted of 1112 events of unidirectionally agonistic interaction and 60 sessions of behavioural experiments. In these sessions, there were 325 phases lasting more than 30 s during which at least two individuals foraged in the patch. The mean phase duration was 55.11 s (SD: 26.38). Overall, we analysed vigilance by 127 individuals (mature females in 2018 and 2019: N = 27 and 40, respectively; mature males in 2018 and 2019: N = 3 and 4, respectively; immature females in 2018 and 2019: N = 21 and 29, respectively; immature males in 2018 and 2019: N = 20 and 22, respectively). The cumulative total number of individuals for both analyses of the proportion of time spent vigilant and vigilance frequency was 929. The mean sample size for each individual was 7.31 (SD: 9.53). The mean percentage of time spent vigilant and vigilance frequency was 18.47% and 0.13 bouts/s, respectively (SD: 15.75 and 0.10).

Statistical Analyses

We used the following two measures as indicators of vigilance level: the proportion of time spent vigilant and the frequency of vigilance. These are the two most commonly used indicators of vigilance level in previous studies (the proportion of time spent vigilant: e.g. Kutsukake, 2006; Watson et al., 2015; Busia, Schaffner, & Aureli, 2016; the frequency of vigilance: e.g. Gould, Fedigan, & Rose, 1997; McNelis & Boatright-Horowitz, 1998; Teichroeb & Sicotte, 2012; for a review, see Allan & Hill, 2018). For each indicator, we tested our predictions regarding the effects of the quality of social relations on vigilance levels.

We analysed the data using generalized linear mixed models (GLMMs; glmer function in the lme4 package) in R ver. 4.0.5 (R Core Team, 2021). In all GLMM analyses, we included the phases and identities of individuals as random effects to deal with pseudoreplication.

For the analysis of the proportion of time spent vigilant (response variable: total duration spent vigilant during each experimental phase; offset term: the log-transformed value of the duration of the experimental phase), we ran a GLMM with a gamma error structure and a log link function. For the analysis of vigilance frequency, we applied a GLMM with a Poisson error structure and log link function (response variable: number of vigilance bouts in an experimental phase; offset term: the log-transformed value of the duration of the experimental phase). We included the following key predictors as fixed effects: the composition of neighbours (categorical: kin-majority neighbours or kin-minority neighbours; relevant to Predictions 1 and 2; see above for definition); the number of neighbours (continuous; relevant to Prediction 2); a two-way interaction between the number and composition of neighbours (relevant to Prediction 2); an individual's absolute dominance rank (continuous; relevant to Prediction 3); and the presence of higher-ranked nonkin neighbours (categorical: present or absent; relevant to Prediction 4). We regarded each individual foraging in the patch as an independent focal individual. All individuals foraging in the patch at the same time as the focal individual were considered neighbours. A neighbour was considered kin if it had a close maternal relationship (i.e. mother, offspring, grandmother, grandoffspring or maternal sibling) with the focal individual. This kinship criterion was set with reference to the study by Chapais et al. (1997), which showed that there is a threshold for nepotism in Japanese monkeys, i.e. there is nepotism in mother–offspring, maternal sibling and grandmother–grandoffspring dyads, but not in aunt–niece dyads. Another study also showed higher rates of tolerated cofeeding above the aunt–niece level of kinship (Belisle & Chapais, 2001). To control for possible confounding effects, we included the following factors as control variables: focal individual's age (categorical: mature or immature) and sex (categorical); the two-way interaction between age and sex; the two-way interaction between rank and composition of neighbours; and the presence of immature offspring in the patch (categorical: present or absent). We fitted all possible combinations of fixed effects. For all models, we calculated and compared the Akaike information criterion (AIC) scores using the dredge function in the MuMIn package in R. The model with the lowest AIC score was considered the best model, i.e. the model that provides a satisfactory explanation of the variation in the data. However, models with a ΔAIC (the difference between model AIC score and that of the best model) < 2 are considered to have a similar level of statistical support as the best model (Burnham & Anderson, 2002). To deal with this uncertainty in model selection, we used a multimodel inference method (Burnham & Anderson, 2002). Akaike weights represent the relative likelihood of each model (Burnham & Anderson, 2002). Using Akaike weights, we calculated the relative variable importance (RVI) of models with ΔAIC < 2 (Burnham & Anderson, 2002). This procedure allowed us to estimate the strength of the relationship between each explanatory variable and the response variables while simultaneously considering the relative likelihood of each model. In cases where a two-way interaction between the number and composition of neighbours remained in the best model, we conducted post hoc analyses to assess the statistical significance of the simple slopes of the number of neighbours and the simple effects of the composition of neighbours. This analysis allowed us to examine whether, given a certain value of one of the interaction terms, the effect of the other term was significant. For the post hoc analyses, we set our alpha level to 0.05.

To reassess the effect of kinship on vigilance levels, we conducted follow-up analyses, which followed all of the above procedures except that we used models including the proportion of kin neighbours (continuous) instead of the composition of neighbours. The proportion of kin was calculated by dividing the number of mature kin neighbours by the sum of the numbers of mature kin and mature nonkin neighbours plus one. The mean percentage of kin was 11% (SD 20; minimum: 0%; maximum: 67%).

Ethical Note

This study was observational and noninvasive. We conducted this study in accordance with the SOKENDAI ethical guidelines for animal research. All observation protocols adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.

Results

The model for the proportion of time spent vigilant with the lowest AIC score contained the number of neighbours, the composition of neighbours, the interaction between these two factors and the presence of higher-ranked neighbours (Table 1). Post hoc Tukey's tests showed that in cases where there were three or more individuals in the patch, the proportion of time spent vigilant was lower when kin constituted the majority of neighbours compared to when they were in the minority (Table 2, Fig. 1a; Prediction 1 supported only if there were three or more neighbours). Sidak post hoc tests showed that in cases where an individual was surrounded by kin-majority neighbours, the 95% confidence interval of the simple slope of the number of neighbours did not include 0 (Table 2). Conversely, in cases where an individual was surrounded by kin-minority neighbours, the 95% confidence intervals of the simple slope of the number of neighbours included 0 (Table 2). These results suggest that, if kin constituted the majority of neighbours, the vigilance level decreased as the number of neighbours increased (Fig. 1a; consistent with Prediction 2). However, if kin were in the minority, then the number of neighbours had no significant effect on vigilance levels (Fig. 1a). Prediction 3 was not supported by the analysis of the proportion of time spent vigilant, since an individual's absolute dominance rank was not included in the best model. Although we predicted that vigilance levels would increase in the presence of higher-ranked neighbours, the results showed that vigilance levels decreased in such situations (Table 2, Fig. 1b; Prediction 4 was not supported). The low Akaike weights produced by the best model ($wi = 0.37$) indicate that there was a considerable degree of uncertainty in model selection. Indeed, there were five models with ΔAIC values < 2 (Table 3). Nevertheless, multimodel inference analyses supported the above results. The RVIs for the number of neighbours, the composition of neighbouring individuals and the interaction of these reached the maximum value (i.e. RVI = 1.0; Table 4). This implies that the proportion of time spent vigilant was more affected by these factors than by others (Table 4). The RVI for the presence of higher-ranked neighbours had the next highest value (RVI = 0.84).

Regarding vigilance frequency, the key predictors included in the model with the lowest AIC scores were the composition of neighbours, dominance rank and presence of higher-ranked neighbours. The best model indicated that the frequency of vigilance when the majority of neighbours were kin was lower than when they were in the minority (Fig. 2a; Prediction 1 supported). In terms of the dominance rank, lower-ranked individuals engaged in vigilance more frequently (Fig. 2b; Prediction 3 supported). Although we predicted that vigilance levels would increase in the presence of higher-ranked neighbours, the results showed that the vigilance frequency decreased in such situations (Table 5, Fig. 2c; Prediction 4 not supported). The interaction between the number and composition of neighbours was not in the best models (Prediction 2 not supported). These results were corroborated by multimodel inference analyses. The Akaike weight of the best model was low ($wi = 0.17$; Table 3) and there were 10 models with ΔAIC values < 2 (Table 3), indicating that there was a considerable degree of uncertainty in model selection. Nevertheless, the RVIs for the composition of neighbouring individuals and the dominance rank had the maximum value (i.e. RVI = 1.0; Table 4). This indicates that the frequency of vigilance was more strongly affected by these factors than by others (Table 4). The value of RVI for one control factor (i.e. age class) also reached its maximum value (Table 4). The RVI for the presence of a higher-ranked neighbour had the next highest (RVI = 0.53; Table 4).

The results of the follow-up analyses using models including the proportion of kin neighbours instead of the composition of neighbours were consistent with the abovementioned results. The

proportion of time spent vigilant decreased as the number of neighbours increased when the proportion of kin was high (Tables A1 and A3, Fig. A1). Regarding vigilance frequency, higher-ranked individuals engaged in vigilance less frequently when the proportion of kin was high, but this was not the case for lower-ranked individuals (Tables A2 and A3, Fig. A2).

Table 1

Factors affecting the proportion of time spent vigilant

Best model	Estimate	SE
Model selection: NN + CN + NN*CN + HRN		
LogLik = −2926.48, AIC = 5868.97		
Intercept	−1.007	0.219
Number of neighbours	−0.345	0.093
Composition (kin-majority > kin-minority)	−0.562	0.228
Number of neighbours*Composition (kin-minority)	0.277	0.095
Higher-ranked neighbour (absent > present)	−0.160	0.083

Cumulative total number of individuals: 929. NN: number of neighbours; CN: composition of neighbours; HRN, higher-ranked neighbour.

Table 2

Results of Sidak post hoc tests of the simple slopes of the number of neighbours relative to the composition of the neighbours, and of Tukey's post hoc tests of the simple effects of the composition of neighbours relative to the number of the neighbours

	Estimates	SE	LCL	UCL
Simple slopes of the number of neighbours				
Kin-majority	−0.345	0.093	−0.552	−0.138
Kin-minority	−0.068	0.036	−0.148	0.012
Simple effects of the composition of neighbours			**Z**	**P**
Kin-majority − kin-minority*neighbours = 1	0.285	0.148	1.931	0.054
Kin-majority − kin-minority*neighbours = 2	0.008	0.099	0.081	0.936
Kin-majority − kin-minority*neighbours = 3	−0.269	0.126	−2.135	0.033
Kin-majority − kin-minority*neighbours = 4	−0.546	0.200	−2.729	0.006

For the Sidak and Tukey tests, we used the functions emtrends and emmeans in the R package emmeans, respectively. LCL and UCL, lower and upper confidence limits, respectively, of the 95% confidence interval.

Table 3

Details of the models with ΔAIC < 2

Models	df	AIC	ΔAIC	w_i
Proportion of time vigilant				
NN + CN + HRN + NN*CN	8	5868.97	0.00	0.37
NN + CN + NN*CN	7	5870.63	1.66	0.16
NN + CN + HRN + Rank + NN*CN	9	5870.68	1.71	0.16
NN + CN + HRN + Sex + NN*CN	9	5870.75	1.78	0.15
NN + CN + HRN + ON + NN*CN	9	5870.77	1.80	0.15
Vigilance frequency				
CN + Rank + Age + HRN	7	4734.60	0.00	0.17
CN + Rank + Age	6	4734.89	0.29	0.15
CN + Rank + Age + HRN + Rank*CN	8	4735.26	0.66	0.12
CN + Rank + Age + Rank*CN	7	4735.48	0.88	0.11
CN + Rank + Age + NN	7	4736.02	1.42	0.08
CN + Rank + Age + HRN + NN	8	4736.05	1.45	0.08
CN + Rank + Age + HRN + Sex	8	4736.17	1.57	0.08
CN + Rank + Age + HRN + ON	8	4736.18	1.58	0.08
CN + Rank + Age + Sex	7	4736.36	1.76	0.07
CN + Rank + Age + ON	7	4736.44	1.84	0.07

Models with ΔAIC > 2 are not presented. AIC: Akaike information criterion; w_i, Akaike weight; NN: number of neighbours; CN: composition of neighbours; HRN: higher-ranked neighbour; ON: offspring neighbour; Age is a categorical variable (mature or immature).

Table 4

Relative variable importance (RVI) calculated from models with ΔAIC < 2

	Proportion of time	Frequency
NN	1.00	0.16
CN	1.00	1.00
NN*CN	1.00	0.00
Rank	0.16	1.00
HRN	0.84	0.53
Sex	0.15	0.15
ON	0.15	0.14
Rank*CN	0.00	0.23
Age	0.00	1.00

NN: number of neighbours; CN: composition of neighbours; HRN: higher-ranked neighbour; ON: offspring neighbour. Age is a categorical variable (mature or immature). Variables that were omitted in the models with ΔAIC < 2 are not shown.

Table 5

Factors affecting the frequency of vigilance

Best model	Estimate	SE
Model selection: CN + Rank + Age + HRN		
LogLik = −2360.30, AIC = 4734.60		
Intercept	−2.320	0.111
Composition (kin-majority < kin-minority)	0.236	0.060
Rank	0.008	0.002
Higher-ranked neighbours (absent > present)	−0.072	0.047
Age (mature > immature)	−0.312	0.087

Cumulative total number of individuals 929. CN: composition of neighbours; HRN, higher-ranked neighbour. Age is a categorical variable (mature or immature).

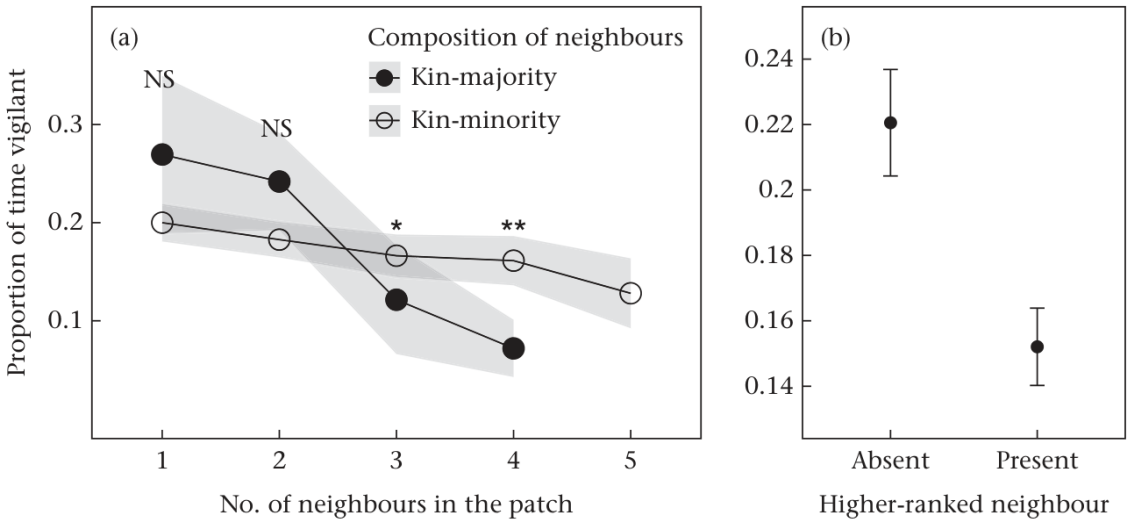


Figure 1. The proportion of time spent vigilant according to the fixed effects (a) number and composition of neighbours and (b) presence of a higher-ranked neighbour. In (a), the black dots and shaded areas represent the mean values and 95% confidence intervals (CIs), respectively. In (b), the black dots and error bars represent the mean values and 95% CIs, respectively. *P < 0.05; **P < 0.01 (Tukey's post hoc test).

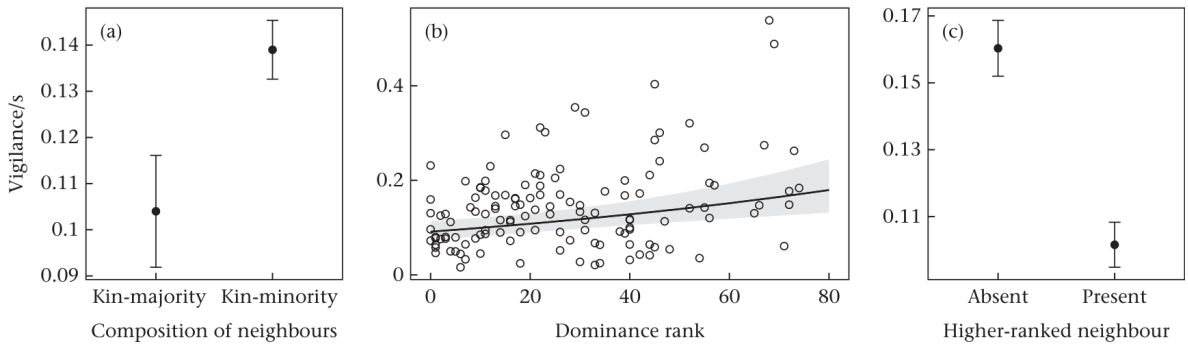


Figure 2. The frequency of vigilance according to the (a) composition of neighbours, (b) dominance rank and (c) presence of a higher-ranked neighbour. In (a) and (c), the black dots and error bars represent the mean values and 95% confidence intervals, CIs, respectively. In (b), smaller numbers on the x-axis indicate a higher ranking in the subject group. The black line and shaded area represent the fitted value and 95% CI, respectively.

Discussion

Vigilance has a trade-off relationship with other adaptive behaviours, such as foraging (e.g. Ebensperger et al., 2006). Hence, animals need to allocate time to vigilance appropriately according to their social status and individual attributes. Overall, our study demonstrated that Japanese macaques regulate their vigilance levels in accordance with the quality of social relationships with neighbours. When there were more than two neighbours, the proportion of time spent on vigilance was lower when kin constituted the majority of neighbours than when they were in the minority (Fig. 1a). The frequency of vigilance decreased when the majority of neighbours were kin (Fig. 2a). This result is consistent with other studies showing that vigilance levels are reduced when kin or individuals with secure relationships are nearby (blue monkeys: Gaynor & Cords, 2012; Geoffroy's spider monkeys: Busia et al., 2019). Like many primate species (e.g. Meikle & Vessey, 1981; Silk,1994), Japanese macaques have strong nepotism and cope with social threats by forming coalitions between close kin (Chapais et al., 1997). In situations where there are many potential allies, the relative risk of social threat might be lower than in situations where they are absent. Hence, individuals may be able to reduce their vigilance levels while relying on the vigilance of potential allies. Note, however, that we classified the composition of neighbours into two categories based on the number of kin and nonkin individuals, without considering the number of immature individuals.

Furthermore, our results implied that the number and composition of neighbours interactively affected vigilance levels. When the majority of neighbours were kin, the proportion of time spent vigilant decreased as the number of neighbours increased (Fig. 1a, Table 2). However, the number of neighbours did not significantly affect vigilance levels when kin were in the minority of neighbours (Fig. 1a, Table 2). Several studies have reported a negative relationship between vigilance levels and the number of neighbours in Japanese macaques (Kazahari & Agetsuma, 2010; Suzuki & Sugiura, 2011). By showing that the effect of the number of neighbours on vigilance levels is modulated by the composition of the neighbours, our results complement the findings of these previous studies. In addition, although many studies have examined the effects of group size or number of neighbours on vigilance levels in primates, the results of these studies have not been consistent (Allan & Hill, 2018). Extrapolating from our results, discrepancies between previous studies might be caused by different social relationship characteristics of different primate species (i.e. whether there is a bias towards making strong social bonds only between kin, whether there is intense intragroup competition, etc.) that modulate the effect of the number of individuals on vigilance level (Kutsukake, 2006; Busia et al., 2019).

Note that we do not claim that the Japanese macaques were precisely counting whether their kin were in the majority or minority of the surrounding individuals. For analysis, we classified

the composition of group members surrounding an individual into two categories (i.e. kin-majority neighbours versus kin-minority neighbours). Although our results showed that the vigilance level of Japanese macaques varied according to this classification of composition, this does not necessarily mean that Japanese macaques accurately calculate the proportion of their kin among their neighbours and determine their level of vigilance accordingly. Presumably, the classification of composition we adopted is not necessarily an exact criterion for Japanese macaques but, rather, roughly corresponds to the relative levels of social risk that affect the physiological and ecological factors that determine the vigilance level (Laundré 2010; Beauchamp, 2017). The results of the follow-up analyses based on the proportion of kin instead of the composition of neighbours were consistent with the above results, suggesting that Japanese macaques relaxed their vigilance when surrounded by kin (Figs A1 and A2).

Our results showed that individuals with lower absolute rankings had higher vigilance levels (Fig. 2b). This is consistent with reports in other primates (patas monkeys, Erythrocebus patas: McNelis & Boatright-Horowitz, 1998; blue monkeys: Gaynor & Cords, 2012; but see Watson et al., 2015). In Japanese macaques, which have a highly despotic society, aggression is almost always directed unilaterally from higher-ranked to lower-ranked individuals. Hence, lower-ranked individuals are likely to encounter social threats more frequently than higher-ranked individuals. Lower-ranked individuals may respond to numerous threats by engaging in frequent vigilance. The follow-up analyses also suggested that, while higher-ranked individuals engaged in vigilance less frequently when the proportion of kin neighbours was high, this was not the case for lower-ranked individuals (Fig. A2). This indicates that low-ranked individuals may not be able to reduce social vigilance irrespective of the number of kin neighbours as potential allies.

We predicted that vigilance levels would increase in Japanese macaques when higher-ranked individuals were nearby. This prediction was consistent with previous studies that have shown that vigilance levels increase when higher-ranked (Gaynor & Cords, 2012), nonaffiliated (Kutsukake, 2006) and hostile individuals (Watts, 1998) are nearby. However, for both the proportion of time spent vigilant and frequency of vigilance, our results demonstrated the opposite relationship between relative rank and vigilance level: the presence of higher-ranked individuals foraging nearby reduced, rather than increased, vigilance levels (Figs. 1b and 2c). This unpredicted result may have been due to our methods for collecting data. We analysed only those periods during which individuals foraged in the patch for more than 30 s without changing their position. This procedure resulted in the exclusion of cases from the analysis such as when a higher-ranked individual entered the patch and immediately caused a lower-ranked individual already there to flee. Hence, there may have been no friction that caused the need for vigilance between individuals that could engage in co-feeding while remaining nearby for a certain amount of time. This is consistent with the fact that, in primates, nearby individuals tend to have strong social bonds with each other (e.g. Silk, 1994). Our results imply that relatively lower-ranked individuals may reduce their vigilance by being in proximity to higher-ranked individuals with whom they have a certain degree of social bond, thus gaining a defence against the rest of the group members. To test this possibility, we must examine whether the social bonds between nonkin pairs predict a flight response by one of the pair when they are nearby, and whether neighbours that can engage in co-feeding while maintaining proximity for a certain amount of time are not targets of vigilance. However, we did not have data on social bonds between nonkin individuals and, as noted in other studies (e.g. Kutsukake, 2006; Watson et al., 2015), it is difficult to identify vigilance targets in the wild. Therefore, we were unable to address these questions in this study. More detailed studies are needed to examine the impact of the presence of higher-ranked neighbours on vigilance levels.

This study examined within-group and within-individual variations in vigilance levels by focusing on a single provisioned group. In the future, between-group comparisons are needed to identify other factors that affect vigilance levels interactively with the quality of social relationships. First, whether group size and the quality of social relationships interactively affect

vigilance levels is an interesting research topic (see Allan & Hill, 2018). To address this question, it is necessary to compare multiple groups of different sizes. Alternatively, rather than species with constant group sizes, such as the Japanese macaque, species with fission–fusion societies may provide an important perspective. It is also assumed that provisioning affected the vigilance levels in our subject group. As provisioning allows individuals in our subject group to acquire food regularly, they were less motivated to forage compared with individuals living in the nonprovisioned group and may have been able to allocate more time to vigilance. To examine the influence of motivation to forage on vigilance levels, it is necessary to quantify the amount of food remaining in the patch and to determine whether the amount was sufficient for individuals. However, it was difficult to quantify the amount of food consumed in the patch based on the video footage. As individuals were able to acquire food outside the patch, it was also difficult to quantify the extent to which they were motivated to forage when they entered the patch. More controlled studies are needed to clarify the relationship between motivation to forage and vigilance levels. Moreover, although the food was placed in clearly visible locations in the patch in our experimental context, individuals in a natural context must search for food, which costs time and energy. In natural contexts, some individuals scan their surroundings to scrounge for food found by others without incurring the cost associated with searching for food. The influence of the so-called 'producer–scrounger' interaction on vigilance levels in the context of foraging is also interesting (e.g. Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991).

We did not make specific predictions for each of the different indicators of vigilance levels (i.e. proportion of time spent vigilant and frequency of vigilance). However, our results suggest that social factors affected the proportion of time spent vigilant and the frequency of vigilance differently. Although absolute dominance ranking affected the frequency of vigilance (Tables 4 and 5), it did not affect the proportion of time spent vigilant (Tables 1 and 4). Conversely, the number of neighbours affected the proportion of time spent vigilant (at least when the majority of neighbours were kin; Tables 1 and 4) but not the frequency of vigilance (Tables 4 and 5). A possible explanation for this is that the frequency of vigilance may reflect the need to judge the immediate social risk surrounding an individual, whereas the proportion of time spent vigilant may be related to the collection of detailed information about the surrounding situation. Thus, the proportion of time spent vigilant may have a more direct trade-off with time budgets for other adaptive behaviours, such as foraging. In cases such as when the majority of neighbours are kin which share social risks, greater numbers of neighbours may mean that it is more efficient to spend time on foraging than on vigilance. Identifying which factors influence individual vigilance levels is important for elucidating animals' adaptive tactics, but it is necessary to consider the ecological implications of each indicator without making a blanket statement about them.

Author Contributions

S.I. and N.K. conceived and designed the study. S.I. gathered the data, performed the statistical analyses, and wrote the article.

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References

Alberts, S. C. (1994). Vigilance in young baboons: Effects of habitat, age, sex and maternal rank on glance rate. Animal Behaviour, 47(4), 749–755. https://doi.org/10.1006/anbe.1994.1107

Allan, A. T. L., & Hill, R. A. (2018). What have we been looking at? A call for consistency in studies of primate vigilance. American Journal of Physical Anthropology, 165, 4–22. https://doi.org/10.1002/ajpa.23381

Beauchamp, G. (2017). What can vigilance tell us about fear? Animal Sentience, 15(1), 1–31.

Bekoff, M. (1995). Vigilance, flock size, and flock geometry: Information gathering by western evening grosbeaks (Aves, Fringillidae). Ethology, 99(1–2), 150–161. https://doi.org/10.1111/j.1439-0310.1995.tb01096.x

Belisle, P., & Chapais, B. (2001). Tolerated co-feeding in relation to degree of kinship in Japanese macaques. Behaviour, 138(4), 487–509. https://doi.org/10.1163/156853901750382124

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: a Practical Information-theoretic Approach (2nd ed.). New York, NY: Springer-Verlag.

Busia, L., Schaffner, C. M., & Aureli, F. (2016). Watch out or relax: Conspecifics affect vigilance in wild spider monkeys (Ateles geoffroyi). Behaviour, 153(1), 107–124. https://doi.org/10.1163/1568539X-00003329

Busia, L., Schaffner, C. M., & Aureli, F. (2019). Watch out! Insecure relationships affect vigilance in wild spider monkeys (Ateles geoffroyi). Behavioral Ecology and Sociobiology, 73(12). https://doi.org/10.1007/s00265-019-2773-x

Caine, N. G., & Marra, S. L. (1988). Vigilance and social organization in two species of primates. Animal Behaviour, 36(3), 897–904. https://doi.org/10.1016/S0003-3472(88)80172-6

Chance, M. R. A. (1967). Attention structure as the basis of primate rank orders. Man, 2(4), 503–518. https://doi.org/10.2307/2799336

Chapais, B. (1988). Experimental matrilineal inheritance of rank in female Japanese macaques. Animal Behaviour, 36(4), 1025–1037. https://doi.org/10.1016/S0003-3472(88)80062-9

Chapais, B., Gauthier, C., Prud'homme, J., & Vasey, P. (1997). Relatedness threshold for nepotism in Japanese macaques. Animal Behaviour, 53(5), 1089–1101. https://doi.org/10.1006/anbe.1996.0365

Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S., et al. (1999). Selfish sentinels in cooperative mammals. Science, 284(5420), 1640–1644. https://doi.org/10.1126/science.284.5420.1640

Ebensperger, L. A., Hurtado, M. J., & Ramos-Jiliberto, R. (2006). Vigilance and collective detection of predators in degus (Octodon degus). Ethology, 112(9), 879–887. https://doi.org/10.1111/j.1439-0310.2006.01242.x

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. Neuroscience & Biobehavioral Reviews, 24(6), 581–604. https://doi.org/10.1016/S0149-7634(00)00025-7

Enari, H. (2014). Snow tolerance of Japanese Macaques inhabiting high-latitude mountainous forests of Japan. In N. B. Grow, S. Gursky-Doyen, & A. Krzton (Eds.), High Altitude Primates (pp. 133–151). New York: Springer. https://doi.org/10.1007/978-1-4614-8175-1_8.

Favreau, F. R., Goldizen, A. W., & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proceedings of the Royal Society B: Biological Sciences, 277(1690), 2089–2095. https://doi.org/10.1098/rspb.2009.2337

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution, 7(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gaynor, K. M., & Cords, M. (2012). Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. Animal Behaviour, 84(3), 531–537. https://doi.org/10.1016/j.anbehav.2012.06.003

Gosselin-ildari, A. D., & Koenig, A. (2012). The effects of group size and reproductive status on vigilance in captive Callithrix jacchus. American Journal of Primatology, 74(7), 613–621. https://doi.org/10.1002/ajp.22013

Gould, L., Fedigan, L. M., & Rose, L. M. (1997). Why be vigilant? The case of the alpha animal. International Journal of Primatology, 18(3), 401–414. https://doi.org/10.1023/A:1026338501110

Hirsch, B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (Cebus apella). Behavioral Ecology and Sociobiology, 52(6), 458–464. https://doi.org/10.1007/s00265-002-0536-5

Iida, T. (1999). Predation of Japanese macaque Macaca fuscata by mountain hawk eagle Spizaetus nipalensis. Japanese Journal of Ornithology, 47(3), 125–127. https://doi.org/10.3838/jjo.47.125

Iki, S., & Kutsukake, N. (2021). Social bias affects vigilance contagion in Japanese macaques. Animal Behaviour, 178, 67–76. https://doi.org/10.1016/j.anbehav.2021.05.019

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behavioral Ecology, 2(2), 143–155. https://doi.org/10.1093/beheco/2.2.143

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. Primates, 50(4), 343–356. https://doi.org/10.1007/s10329-009-0153-2

Kazahari, N., & Agetsuma, N. (2010). Mechanisms determining relationships between feeding group size and foraging success in food patch use by Japanese macaques (Macaca fuscata). Behaviour, 147(11), 1481–1500. https://doi.org/10.1163/000579510X521573

Kudo, H., & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. Animal Behaviour, 62(4), 711–722. https://doi.org/10.1006/anbe.2001.1808

Kutsukake, N. (2000). Matrilineal rank Inheritance varies with absolute rank in Japanese macaques. Primates, 41(3), 321–335. https://doi.org/10.1007/BF02557601

Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. Ethology, 112(6), 581–591. https://doi.org/10.1111/j.1439-0310.2006.01200.x

Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. International Journal of Primatology, 28(4), 907–918. https://doi.org/10.1007/s10764-007-9156-2

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. The Open Ecology Journal, 3(1), 1–7. https://doi.org/10.2174/1874213001003030001

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: The group-size effect. Animal Behaviour, 49(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Mac Carron, P., & Dunbar, R. I. M. (2016). Identifying natural grouping structure in gelada baboons: A network approach. Animal Behaviour, 114, 119–128. https://doi.org/10.1016/j.anbehav.2016.01.026

McDougall, P. L., & Ruckstuhl, K. E. (2018). Vigilance behaviour is more contagious when chewing stops: Examining the characteristics of contagious vigilance in bighorn sheep. Behavioral Ecology and Sociobiology, 72(9), 143. https://doi.org/10.1007/s00265-018-2536-0

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. Animal Cognition, 1(1), 65–69. https://doi.org/10.1007/s100710050008

Meikle, D. B., & Vessey, S. H. (1981). Nepotism among rhesus monkey brothers. Nature, 294(5837), 160–161. https://doi.org/10.1038/294160a0

Pannozzo, P. L., Phillips, K. A., Haas, M. E., & Mintz, E. M. (2007). Social monitoring reflects dominance relationships in a small captive group of brown capuchin monkeys (Cebus apella). Ethology, 113(9), 881–888. https://doi.org/10.1111/j.1439-0310.2007.01392.x

Pulliam, H. R. (1973). On the advantages of flocking. Journal of Theoretical Biology, 38(2), 419–422. https://doi.org/10.1016/0022-5193(73)90184-7

R Core Team. (2021). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Roberts, S. J., & Cords, M. (2013). Group size but not dominance rank predicts the probability of conception in a frugivorous primate. Behavioral Ecology and Sociobiology, 67(12), 1995–2009. https://doi.org/10.1007/s00265-013-1607-5

Silk, J. B. (1994). Social relationships of male bonnet macaques: Male bonding in a matrilineal society. Behaviour, 130(3–4), 271–291. https://doi.org/10.1163/156853994X00569

Silk, J. B. (2002). Using the 'F'-Word in primatology. Behaviour, 139(2), 421–446. https://doi.org/10.1163/156853902760102735

Suzuki, M., & Sugiura, H. (2011). Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. American Journal of Primatology, 73(7), 623–631. https://doi.org/10.1002/ajp.20937

Takahashi, H. (1997). Huddling relationships in night sleeping groups among wild Japanese macaques in Kinkazan Island during winter. Primates, 38(1), 57–68. https://doi.org/10.1007/BF02385922

Takahata, Y., Huffman, M. A., Suzuki, S., Koyama, N., & Yamagiwa, J. (1999). Why dominants do not consistently attain high mating and reproductive success: A review of longitudinal Japanese macaque studies. Primates, 40(1), 143–158. https://doi.org/10.1007/BF02557707

Teichroeb, J. A., & Sicotte, P. (2012). Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (Colobus vellerosus). Behavioral Ecology and Sociobiology, 66(3), 453–466. https://doi.org/10.1007/s00265-011-1292-1

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, & F. B. M. de Waal (Eds.), Natural Conflict Resolution (pp. 106–128). Berkeley, CA: University of California Press.

Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. Animal Behaviour, 55(4), 1063–1069. https://doi.org/10.1006/anbe.1997.0636

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. Animal Behaviour, 60(6), 711–722. https://doi.org/10.1006/anbe.2000.1528

van Schaik, C. P. (1983). Why are diurnal primates living in groups? Behaviour, 87(1–2), 120–144. https://doi.org/10.1163/156853983X00147

Vickery, W., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producer, scroungers, and group foraging. The American Naturalist, 137(6), 847–863. https://doi.org/10.1086/285197

Watson, K. K., Li, D., Brent, L. J. N., Horvath, J. E., Gonzalez-Martinez, J., Ruíz-Lambides, A. V., et al. (2015). Genetic influences on social attention in freeranging rhesus macaques. Animal Behaviour, 103, 267–275. https://doi.org/10.1016/j.anbehav.2015.02.012

Watts, D. P. (1998). A preliminary study of selective visual attention in female mountain gorillas (Gorilla gorilla beringei). Primates, 39(1), 71–78. https://doi.org/10.1007/BF02557744

Wheeler, B. C., Scarry, C. J., & Koenig, A. (2013). Rates of agonism among female primates: A cross-taxon perspective. Behavioral Ecology, 24(6), 1369–1380. https://doi.org/10.1093/beheco/art076

Zhao, J. M., Lyu, N., Sun, Y. H., & Zhou, L. Z. (2019). Number of neighbors instead of group size significantly affects individual vigilance levels in large animal aggregations. Journal of Avian Biology, 50(4), 1–11. https://doi.org/10.1111/jav.02065

Appendix

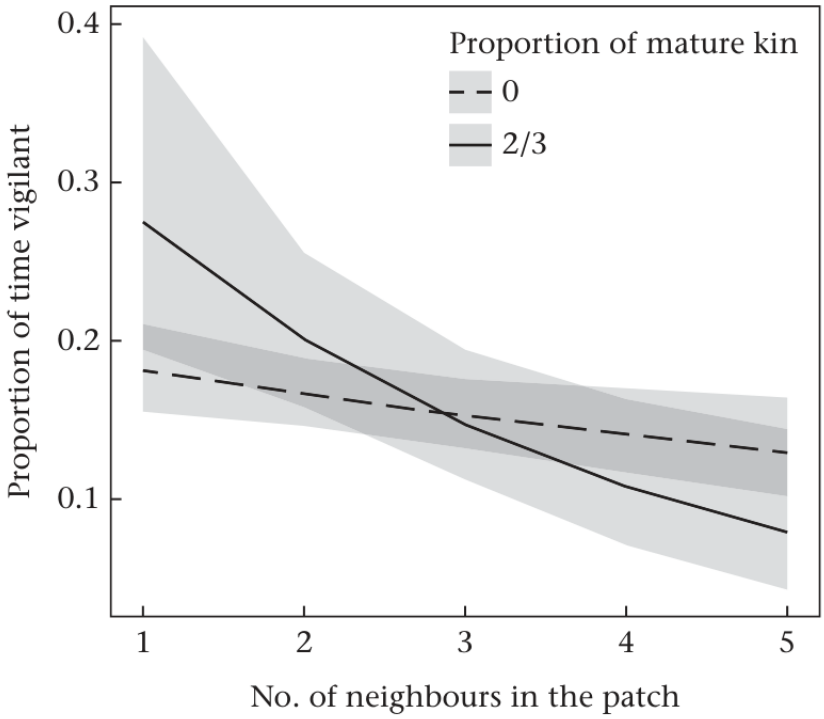


Figure A1. The proportion of time spent vigilant according to the number of neighbours and proportion of kin. The solid and dashed lines are the values predicted by the best model (Table A1) at the maximum (i.e. 2/3) and minimum (i.e. 0) values of the proportion of kin, respectively. The shaded areas indicate the 95% confidence intervals.

Table A1

Factors affecting the proportion of time spent vigilant

Best model	Estimate	SE
Model selection NN + PK + NN*PK		
LogLik = −2930.53, AIC = 5875.07		
Intercept	−1.624	0.100
Number of neighbours	−0.085	0.036
Proportion of kin	0.962	0.422
Number of neighbours*Proportion of kin	−0.340	0.167

Only the best model is shown. We included the proportion of kin (continuous) as a fixed effect, instead of the categorical composition of neighbours variable (majority neighbours versus kin-minority neighbours). Cumulative total number of individuals 929. NN: number of neighbours; PK: proportion of kin; HRN: higher-ranked neighbour.

Table A2

Factors affecting the frequency of vigilance

Best model	Estimate	SE
Model selection PK + Rank + PK*Rank + Age + HRN		
LogLik = −2358.55, AIC = 4733.09		
Intercept	−2.057	0.095
Proportion of kin	−0.717	0.169
Rank	0.007	0.002
Proportion of kin*Rank	0.015	0.007
Higher-ranked neighbours (absent > present)	−0.085	0.047
Age (mature > immature)	−0.307	0.089

Only the best model is shown. We included the proportion of kin (continuous) as a fixed effect, instead of the categorical composition of neighbours variable (majority neighbours versus kin-minority neighbours). Cumulative total number of individuals 929. PK: proportion of kin; HRN: higher-ranked neighbour.

Table A3

Relative variable importance (RVI) calculated from models with ΔAIC < 2

	Proportion of time	Frequency
NN	1.00	0.14
PK	0.59	1.00
NN*PK	0.52	0.00
Rank	0.11	1.00
HRN	0.53	0.81
Sex	0.12	0.16
ON	0.12	0.16
Rank*PK	0.00	1.00
Age	0.06	1.00

We included the proportion of kin (continuous) as a fixed effect, instead of the categorical composition of neighbours variable (majority neighbours versus kin-minority neighbours). NN: number of neighbours; PK: proportion of kin; HRN: higher-ranked neighbour; ON: offspring neighbour. Age is a categorical variable (mature or immature). Variables that were omitted in the models with ΔAIC < 2 are not shown.

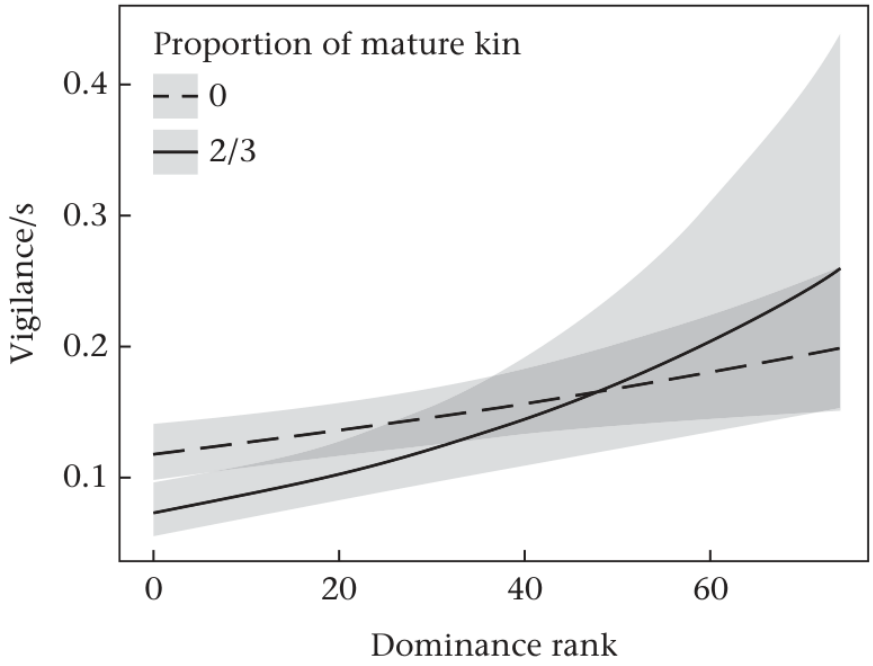


Figure A2. The frequency of vigilance according to the proportion of kin and dominance rank. The solid and dashed lines represent the values predicted by the best model (Table A2) at the maximum (i.e. 2/3) and minimum (i.e. 0) values of the proportion of kin, respectively. The shaded areas are the 95% confidence intervals. Smaller numbers on the x-axis indicate a higher ranking in the subject group.