Watch out or relax: conspecifics affect vigilance in wild spider monkeys (*Ateles geoffroyi*)

Laura Busia[1], Colleen M. Schaffner[1] & Filippo Aureli[1,2]

[1]Instituto de Neuroetologia, Universidad Veracruzana,
Xalapa, Veracruz, Mexico

[2]Research Centre in Evolutionary Anthropology and Palaeoecology,
Liverpool John Moores University, Liverpool, United Kingdom

Abstract

In most animal species, predation risk is considered the main factor affecting vigilance, and an individual is expected to spend less time vigilant in larger than in smaller groups. However, vigilance patterns in primates appear to differ, with no consistency in group-size effects. As individuals in highly gregarious species such as diurnal primates face frequent threats from group members, there may be increased vigilance in larger groups to monitor conspecifics rather than or in addition to predators. We tested this hypothesis in wild spider monkeys, which live in communities but fission and fuse in subgroups of variable size and membership throughout the same day. We found no overall effect of subgroup size, as traditionally measured, on vigilance. However, a possible explanation is that vigilance may be effectively shared only with individuals in close proximity, rather than with all subgroup members. We found that a larger number of neighbours (i.e., subgroup members within 5m) was associated with a lower proportion of time individuals spent vigilant, which is similar to findings in other studies. Another social factor that may affect individuals’ vigilance is the possibility of between-community encounters. Higher levels of vigilance can be expected in areas closer to the boundary of the home range, where between-community encounters are more likely to occur compared with non-boundary areas. We found that location in terms of boundary vs. non-boundary areas had a significant effect on the time individuals spent vigilant in the expected direction. We also found that location modulated the effect of subgroup size on vigilance; only in the boundary areas did larger subgroup sizes result in less individual vigilance time. We concluded that conspecifics affect vigilance of wild spider monkeys in multiple ways.

Keywords: vigilance, subgroup size, neighbours, boundary areas, *Ateles*

Introduction

Anti-predatory benefits have long been considered a major factor driving group living (Alexander, 1974; van Schaik, 1983; Elgar, 1989; Roberts, 1996; Bettridge & Dunbar, 2012). One of the major advantages of group living is thought to be easier detection of predators in large rather than small groups (“many-eyes hypothesis” van Schaik & van Hooff, 1983; long-tailed macaques, *Macaca fascicularis*, van Schaik et al., 1983; Elgar, 1989; dark-eyed juncos, *Junco hyemalis* and American tree sparrows, *Spizella arborea*, Lima, 1995; Bednekoff & Lima, 1998; meerkats, *Suricata suricata*, Clutton-Brock et al., 1999, elk, *Cervus elaphus*, Childress & Lung, 2003; Columbian ground squirrels, *Spermophilus columbianus*, Fairbanks & Dobson, 2006), because there are more individuals that can scan for predators. For example, birds in larger flocks detect predators sooner and as a result fly away from them from a larger distance than birds in smaller flocks (starlings, *Sturnus vulgaris*, Powell, 1974; white-fronted geese, *Anser albifrons*, Lazarus, 1978; quelea, *Quelea quelea,* Lazarus, 1979). In an experimental study, the detection of potential predators occurred earlier in larger than in smaller groups of long-tailed macaques (van Schaik et al., 1983). In addition, among wild yellow baboons (*Papio cynocephalus*), individuals in smaller groups stayed closer to large trees than individuals in larger groups, because of their difficulty in detecting terrestrial predators, such as lions (*Panthera leo*), leopards (*P. pardus*) and hyenas (*Crocuta crocuta*) (Stacey, 1986).

In vigilance studies, vigilance is defined as the individual monitoring its surroundings beyond its arm’s reach (reviewed in Treves, 2000). Living in large groups may allow individuals to decrease their own vigilance level without lessening the group’s collective ability to detect predators (Pulliam, 1973; Elgar, 1989; dark-eyed juncos and American tree sparrows, Lima, 1995; Bednekoff & Lima, 1998; meerkats, Clutton-Brock et al., 1999; elk, Childress & Lung, 2003; Columbian ground squirrels, Fairbanks & Dobson, 2006). However, across primate species, researchers often find no association between group size and individual vigilance (as reviewed by Treves, 2000). This may be because researchers do not always take into account other factors that might affect the relationship between group size and vigilance (Elgar, 1989; Treves, 2000; Beauchamp, 2008). For example, individuals also use vigilance to monitor conspecifics (Chance, 1967; patas monkey, *Erythrocebus patas,* McNelis &

Boatright-Horowitz, 1998; red colobus, *Piliocolobus tephrosceles,* and red-tail monkey, *Cercopithecus ascanius,* Treves, 1998, 1999, 2000; Evers et al., 2012). Monitoring conspecifics is useful during the mating season, to avoid same-sex competitors or to find potential mates (desert baboons, *Papio cynocephalus ursinus*, Cowlishaw, 1998; black howler monkeys, *Alouatta pigra,* Treves, 1998; see also adult male giraffes, *Giraffa camelopardalis*, Cameron & du Toit, 2005; adult male elk, Lung & Childress, 2007; European rabbits, *Oryctolagus cuniculus*, Monclus & Rodel, 2008). Furthermore, within-group aggression rates are considered higher in primates than in other taxa (Treves, 2000), which may explain why this taxonomic group does not always follow the expected antipredator patterns for vigilance. Despite the risk of within-group aggression, individuals in close proximity (hereafter neighbours) do not usually represent a threat, as individuals that are often neighbours are usually compatible partners (*sensu* Cords & Aureli, 2000; e.g. bonnet macaques, *Macaca radiata*, Silk, 1994, chimpanzees, *Pan troglodytes,* Fraser et al., 2008; ravens, *Corvus corax,* Fraser & Bugnyar, 2010, barbary macaques, *M. sylvanus*, McFarland & Majolo, 2011). Thus, unlike other subgroup members, neighbours may not require a high degree of monitoring and may even provide benefits in terms of sharing vigilance. For example, individuals with no close neighbours were more vigilant than those with at least one neighbour in red colobus monkey males and red-tail colobus monkey females (Treves, 1998).

Another factor affecting vigilance may be the risk posed by conspecifics from other groups. Between-group relationships in primates are mainly competitive (Wrangham, 1980) and aggressive or even fatal interactions between members of different groups have been reported in many primate species (Cheney, 1987; yellow baboons, Shopland, 1982; Japanese macaques *Macaca fuscata*, Sugiura et al., 2000; black-and-white colobus monkeys, *Colobus guereza*, Fashing, 2001; mountain gorillas, *Gorilla gorilla*, Sicotte, 1993; chimpanzees, Goodall, 1986; Wilson & Wrangham, 2003). Accordingly, the time spent vigilant may be higher in areas of the home range where different groups' home ranges overlap compared to non-overlapping areas, as shown in Thomas's langurs (*Presbytis thomasi,* Steenbeek et al., 1999) and in black and white colobus monkeys (Macintosh & Sicotte, 2009).

Species with a high degree of fission-fusion dynamics live in communities characterized by large temporal variation in cohesion, subgroup composition and subgroup size (Kummer, 1971; Aureli et al., 2008). This social flexibility is widespread across many taxa, both in primates and non-primate species (Aureli et al., 2008). Although researchers commonly focus on the reduction of competition over food as the main explanation for the high degree of fission-fusion dynamics (Kummer, 1971; Symington, 1990; Aureli & Schaffner, 2008; Asensio et al., 2009), several species adjust their grouping patterns through fission-fusion dynamics according to predation risk (dolphins, Karczmarski et al., 2005; bisons, *Bison bison*, Fortin et al., 2009; guppies, *Poecilia reticulate,* Kelley et al., 2011).

1. Given that vigilance is usually considered an anti-predator strategy, few studies have investigated vigilance in species with low predation pressure. Thus, little is known about the role of conspecifics on vigilance in species, in which it is possible to exclude a main role of predation. Spider monkeys represent an excellent candidate species for several reasons. First, spider monkeys' high degree of fission-fusion dynamics provides the opportunity to

evaluate the effects of the number of associating conspecifics on vigilance as subgroup size changes frequently throughout the day. Second, there are relatively few reports of predation events on *Ateles* species (from crested eagle, *Morphnus guianensis*, Julliot, 1994; jaguar, *Panthera onca*, Matsuda & Izawa, 2008; puma, *Puma concolor*, Di Fiore, 2002; two events involving a puma and an unidentified terrestrial predator have been recorded in our study site in 18 years: Ramos-Fernandez, pers. comm.; pers. obs.), indicating that their predation pressure is low. Furthermore, individuals are frequently found alone or in small subgroups (potentially more vulnerable to predation, Hoogland & Sherman, 1976; Bertram, 1978; Foster & Treherne, 1981), suggesting predation pressure has a small role in shaping spider monkey behaviour. Finally, a third reason spider monkeys are a good model to test the role of conspecifics on vigilance is because they may be threatened by other communities of the same species. Spider monkeys are territorial as males patrol their community boundaries (Wallace, 2008), make incursions into the territory of other communities (Aureli et al., 2006) and between-community aggressive encounters have been reported for this taxon (van Roosmalen, 1985; Symington, 1988).

Our aim was to evaluate the role of conspecifics in explaining variation in spider monkey vigilance. First, we examined whether spider monkey vigilance was affected by subgroup size. If the hypothesis that vigilance serves mainly to monitor external threats, such as predators, applies to spider monkeys, we predicted that individuals would spend less time vigilant in larger than in smaller subgroups. Alternatively, given that primates face a higher frequency of within-group aggression compared with other taxa (Treves, 2000) and given that even lethal within-group aggression events have been reported in spider monkeys (Campbell, 2006; Valero et al., 2006), we predicted that individuals would spend more time vigilant in larger than in smaller subgroups in order to monitor a larger number of subgroup members. Second, we evaluated whether the type of conspecifics affected vigilance. Given that vigilance could be shared with neighbours (Treves, 1998), we predicted that, regardless of number of animals in the overall subgroup, the number of neighbours would affect the time spent vigilant. Third, we examined the role of location in terms of the probability of between-community encounters. Given that the risk of between-community encounters is higher at the boundaries of the community home range (Steenbeek et al., 1999; Macintosh & Sicotte, 2009), we predicted that individuals would spend more time vigilant at the boundaries of their territory compared with non-boundary areas. We also predicted that location would play a modulating role in the relationship between subgroup size and vigilance, as the collective ability to detect signs of conspecifics from other communities increases with the number of individuals present in the subgroup.

Methods

Field site and study subjects

The field site is located in the forest surrounding the Punta Laguna lake, within the natural protected area of Otoch Ma'ax Yetel Kooh, Yucatan Peninsula, Mexico (20°38’ N, 87°38’ W). The natural protected area measures 5367 ha and includes a mosaic of old-growth, semi-evergreen medium forest, with trees up to 25 m in height, and 30–50-year-old successional forest (Ramos-Fernandez & Ayala-Orozco, 2003).

The study subjects were 22 individuals of a well-habituated community of spider monkeys (*Ateles geoffroyi*) living in the protected area (6 adult males, 10 adult females, 1 subadult male, 5 subadult females). However, 6 subjects (1 adult male, 3 adult females and 2 subadult females) were observed less than three hours and were therefore not included in the data analysis. Subjects have been part of a continuous long-term project since 1997 and each monkey was individually recognized by facial features and differences in fur coloration. We classified individuals as adults if they were more than 8 years of age and as subadults if they were 5-8 years old. As the birth date was not known for immigrant females, they were classified as subadults until they gave birth for the first time (Shimooka et al., 2008).

Data collection

We observed the monkeys in 4-hour or 8-hour shifts throughout the course of the day. LB and 2 field assistants followed subgroups (hereafter subgroup follow) an average of 5.5 hours a day. Data were collecting by using focal animal sampling (Altmann, 1974). From January to December 2013, 497 15-minute focal samples (mean ± SE: 31.1 ± 2.67 per subject; range: 16-50) were collected by the first author during 750 hours of subgroup follows.

During focal samples the time the subject spent vigilant, defined as the monitoring of the surrounding area beyond arm’s reach and not in the direction of food while foraging (Treves, 2000), was continuously recorded. We also recorded as neighbours all the individuals within 5 m from the focal animal every two minutes. In addition, we also recorded the time the focal animal was out of view or the visibility was too poor to reliably observe vigilance. Focal animals were chosen based on the number of previous focal samples, to have a similar number of focal samples per individual across the subjects. No animal was sampled more than once per hour.

The subgroup size was continuously updated as we identified every member of the subgroup initially encountered each day and recorded all membership changes due to fission and fusion events. An individual was considered part of the followed subgroup if it was <30 m from a subgroup member following a chain rule already established for this study site (Ramos-Fernandez, 2005). Thus, individuals could be spread out over a wide area but still belong to the same subgroup if they were <30m from at least one subgroup member. We recorded fission events when one or more individuals were not seen within 30 m of a subgroup member for 30 minutes. We recorded fusion events when one or more individuals from a different subgroup came within 30 m from any member of the followed subgroup (Rebecchini et al., 2011). Every 20 minutes we recorded the location of the centre of the subgroup with a Garmin GPSmap 76Cx.

Data analyses

Linear mixed models (LMMs) were used to examine the effect of several factors on vigilance. We selected LMMs to allow focal animal identity to be included as a random factor to account for the lack of independence resulting from multiple focal observations on the same individual**.** The dependent variable was the proportion of time the subject spent vigilant in each focal sample. To calculate this proportion the duration the subject was vigilant was divided by the duration of the focal sample minus the time the subject was out of view and the time the visibility was too poor to reliably observe vigilance. We transformed the data with the arcsine of the square root to normalize them (Quinn & Keough, 2002). We entered the following independent variables: subgroup size, number of neighbours and location (boundary or non-boundary areas). Subgroup size was the number of adults and subadults that were present in the subgroup during the focal sample; in cases where fission or fusion events occurred during the focal sample we used the subgroup size occurring for the majority of the focal sample. The number of neighbours was the mean number of neighbours present in the 2-minute scans collected during the focal sample. As subgroup size and number of neighbours are two measures of association between community members, we evaluated the potential correlation between them and the Pearson's correlation coefficient was 0.2 (with a low variance inflation factor of 1.044; O'brien, 2007).

In order to classify the location of the focal animal as boundary area or non-boundary area, we estimated the community home range with GPS data points using the kernel method (Worton, 1989). We considered the area between the 80% and the 95% kernel of the utilization distribution as boundary area and the area within the 80% kernel of the utilization distribution as non-boundary area. In order to test whether location affected vigilance given the differential possibility of between-community encounters, we excluded the focal samples collected at the boundaries along the lake, because no other monkey communities can be present. We also included the interaction between subgroup size and location as an independent variable. In all analyses, the age and sex of the focal animal were included in the LMMs as additional independent variables to control for potentially confounding effects, as well as the subgroup type (mixed sex or unisex). The best models were chosen using the lowest Akaike information criteria (AIC, Richards et al., 2011). All the statistical analyses were carried out using the “nlme” package in R (Pinheiro et al. 2014). We set an alpha level of $p < 0.05$ for all tests.

Results

The best model was the full model that included all independent variables (AIC: -40.27). We found no evidence for subgroup size affecting the proportion of time individuals spent vigilant (Table 1). In contrast, the number of neighbours had a statistically significant effect on the proportion of time individuals spent vigilant (Table 1). A higher number of neighbours was associated with less time spent vigilant (Figure 1).

Figure 1 here

Location also had a significant effect on vigilance: the proportion of time individuals spent vigilant was higher in boundary (mean ± SE: 0.29 ± 0.03) than in non-boundary areas (0.27 ± 0.01; Table 1). In addition, location modulated the effect of subgroup size on vigilance as there was an effect of the interaction between subgroup size and location on the proportion of time individuals spent vigilant (Table 1). To better understand the interaction effect, we ran two further models, one for each location type. Subgroup size had a significant negative relationship with the proportion of time spent vigilant in boundary areas (t_{44}=-2.64; p=0.01, Figure 2), whereas it had no effect in non-boundary areas (t_{419}=0.84; p=0.398, Figure 2). Note that large subgroups (9-12 individuals) have a smaller sample size than small (1- 4 individuals) and medium subgroups (5- 8 individuals) and therefore have less weight in the overall means for boundary and non- boundary areas.

Figure 2 here

Table 1: Results of the best LMM showing the relationship between various independent variables and the proportion of time focal animals spent vigilant**.**

	ß	SE	DF	t	p
Intercept	0.56	0.04	470	14.59	<0.001
Subgroup size	-0.001	0.006	470	-0.19	0.850
Location: boundary vs non-boundary areas	0.16	0.06	470	2.62	0.009
Total neighbours	-0.06	0.01	470	-4.24	<0.001
Subgroup size x Location	-0.03	0.01	470	-2.81	0.005
Age: adults vs subadults	-0.07	0.03	13	-2.48	0.028
Sex: females vs. males	0.06	0.02	13	2.53	0.025
Subgroup type	-0.08	0.03	470	-3.05	0.002

Control variables (i.e. age, sex, subgroup type) also had significant effects (Table 1): subadults were less vigilant than adults; males were more vigilant than females; and individual's vigilance level was higher in mixed-sex than in unisex subgroups.

Discussion

We found no overall relationship between subgroup size and vigilance in wild spider monkeys. This outcome does not support the prediction of lower vigilance when subgroups are larger according to the hypothesis that vigilance serves mainly to monitor external threats, such as predators. Similarly, the result does not provide evidence supporting the prediction of more vigilance when subgroups are larger according to the hypothesis that vigilance serves to monitor group members. By contrast, our findings supported the hypothesis that vigilance can be shared with conspecifics when they are in proximity (within 5 m) as individuals spent less time vigilant when they were with a higher number of neighbours. The hypothesis regarding location, in terms of differential probability of between-community encounters having an effect on vigilance, was also supported as spider monkeys spent more time vigilant in boundary areas compared with non-boundary areas. Our results also showed that location played a modulating role in the relationship between subgroup size and the proportion of time individuals spent vigilant. In boundary areas individuals spent less time vigilant in larger subgroups, while such a relationship was not found in non-boundary areas.

The relationship between overall group size and vigilance in primates is not straightforward (negative effect: wedge capped capuchin monkeys, *Cebus olivaceus,* de Ruiter, 1986; humans, Wirtz & Wawra, 1986; no effect: *Cercopithecus* sp. Cords, 1990; white-faced capuchins, *Cebus capucinus* Rose & Fedigan, 1995; black howler monkeys, Treves et al., 2001), which may be due to potential confounding factors (Elgar, 1989). Our findings revealed that location (boundary areas vs. non-boundary areas) may be a potential confounding factor, as it plays a modulating role in the relationship between subgroup size and vigilance (see below).

The number of neighbours rather than group size per se seems to be a factor affecting vigilance. In many studies, a larger number of group members in proximity was associated with individuals decreasing the proportion of time spent vigilant (desert baboons, Cowlishaw 1998; Thomas's langurs, Steenbeek et al., 1999; black howler monkeys, Treves et al., 2001; saddleback tamarins, *Saguinus fuscicollis,* Smith et al., 2004; moustached tamarins, *S. mystax*, Smith et al., 2004; Stojan-Dolar & Heymann, 2010; eastern grey kangaroos, *Macropus giganteus,* Favreau et al., 2010). Our findings support the latter relationship. This could be due to several mechanisms. Antipredator vigilance could be shared more efficiently among individuals that are in proximity rather than among all group members, as already shown in red-tail and red colobus monkeys (Treves, 1998). Individuals may regulate their vigilance according to the vigilance of other group members (e.g., eastern grey kangaroos, Pays et al., 2007, Favreau et al., 2010; gulls, *Larus* sp., Beauchamp, 2009) and proximity may make individuals more aware of their neighbours' activity compared to that of all subgroup members, thus reducing the need for active monitoring. In addition, the dilution effect might apply more strongly among neighbours than among all subgroup members (e.g. in white-faced capuchins, Philips, 1995; red colobus and red-tail monkeys, Treves, 1998). The perception of a lower risk of predation when individuals have neighbours may lead to lower vigilance levels. Given the multiple reasons to consider neighbours as an important factor affecting individual vigilance, it would be prudent to take into account neighbours in future vigilance studies. Neighbour presence can be thought of as another association level of individuals (in addition to group size, Treves, 1998). If not considered, it could represent a confounding factor in the relationship between vigilance and grouping patterns.

As some studies found the presence of neighbours increased the time individuals spent vigilant (e.g. brown capuchins, Hirsch, 2002; giraffes, Cameron & du Toit, 2005; chimpanzees: Kutsukake, 2007; elk, Lung & Childress, 2007; European rabbits, Monclus & Rodel, 2008), the effect of neighbours on vigilance may be depend on factors such as predation level, the spatial position within the group, seasonality and social relationships, which could be evaluated by future comparative research. For example, most vigilance could be directed to monitoring conspecifics in populations with low predation risk (Hirsch, 2002). The spatial position within the group may also play an important role, as central individuals may be less threatened by predators (e.g. Janson, 1990). In addition, the different effect of neighbours on vigilance may depend on the season in which the study is conducted. For example, the increase in male vigilance as the number of neighbours increase during the breeding season in rabbits may be explained by the need to monitor conspecifics’ activities (Monclus & Rodel 2008). Similarly, the increase in vigilance due to neighbours may be related to reproductive motivation in giraffes (Cameron & du Toit, 2005). Social relationships may also have a key role in determining the difference in vigilance depending on the type of neighbours, as shown in chimpanzees in which an individual was more vigilant when in proximity with more non-affiliative group members (Kutsukake 2006).

Our findings show higher levels of vigilance in boundary compared with non-boundary areas. This is possibly due to the higher risk of between-community encounters in boundary areas than in non-boundary areas (Steenbeek et al., 1999; Macintosh & Sicotte, 2009). The detection of signs of conspecifics from other communities (e.g. canopy movements) through vigilance may then reduce the likelihood of hostile between-community interactions. However, over the years we have witnessed relatively few between-community encounters involving the study community. Thus, we exercise caution in our interpretation. An alternative explanation of our findings may be based on the differential use of the two location types as our boundary areas are by definition areas included between the 80% and the 95% of the utilization distribution. It is possible that individuals need to be more vigilant in areas with a lower degree of use as they are likely less well known and potentially more risky, as demonstrated for captive black tufted-ear marmosets (*Callithrix penicillata,* Dacier et al., 2006). This alternative explanation is not, however, supported by the findings of captive studies in which individuals were relocated or experimentally located and did not show any significant increase in vigilance in the novel environment (black tufted-ear marmosets, Barros et al., 2004; brown capuchin monkeys, *Sapajus apella* and squirrel monkeys, *Saimiri sciureus*, Dufour et al., 2011). Another possible explanation for the difference in vigilance depending on location is that it may be harder for individuals to find food, which would not be the case in novel environments for captive species that are fed ad libitum (Barros et al., 2004; Dufour et al., 2011).

Location in terms of boundary areas vs. non-boundary areas also played a modulating role in the relationship between subgroup size and vigilance in our study. A possible explanation of this modulating role is that a reduction of vigilance effort by sharing it with community members in larger subgroups only occurs in relatively risky areas where the vigilance burden is high, regardless of whether the risk is associated with between-community encounters or less well-known areas. This reduction in individual vigilance, when spider monkeys are in larger subgroups, may also occur because they would be more likely to win a between-community encounter, given the large subgroup size. However, two issues caution us in our interpretation. First, the sample size of large subgroups in boundary areas was small. Second, we did not have information on vigilance targets, such as potential predators, other group members, or escape routes, because it is difficult to distinguish among them.

The findings of our study emphasise the important role of conspecifics on vigilance in a species characterized by a high degree of fission-fusion dynamics and a relatively low predation pressure. The type of relationships with conspecifics (e.g. mainly friendly with neighbours and mainly hostile with members of other communities) may represent a key factor to develop a more comprehensive understanding of vigilance in primate and non-primate species.

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References

Alexander, R.D. (1974). The evolution of social behavior. – Ann. Rev. Ecol. Syst. 5: 325-383.

Altmann, J. (1974). Observational studies of behavior: sampling methods. - Behaviour 49(3): 227-267.

Asensio, N., Korstjens, A.H., Schaffner, C.M. & Aureli, F. (2008). Intragroup aggression, fission fusion dynamics and feeding competition in spider monkeys. - Behaviour 145(7): 983-1001.

Aureli, F., Schaffner, C.M., Verpooten, J., Slater, K. & Ramos-Fernandez, G.

(2006). Raiding parties of male spider monkeys: insights into human warfare? – Am. J. Phys. Anthropol. 131(4): 486-497.

Aureli, F. & Schaffner, C.M. (2008). Social interactions, social relationships and the social system of spider monkeys. - In: Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles. (Campbell, C.J. ed.) Cambridge University Press. p. 236-265.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B. & van Schaik, C.P. (2008). Fission-fusion dynamics: new research frameworks. - Curr. Anthropol. 49(4): 627-654.

Barros, M., Alencar, C. & Tomaz, C. (2004). Differences in aerial and terrestrial visual scanning in captive black tufted-ear marmosets (*Callithrix penicillata*) exposed to a novel environment. - Folia Primatol. 75(2): 85-92.

Beauchamp, G. (2008). What is the magnitude of the group-size effect on vigilance? - Behav. Ecol. 19(6): 1361-1368

Beauchamp, G. (2009). Sleeping gulls monitor the vigilance behaviour of their neighbours. - Biol. Lett. 5(1): 9-11.

Bednekoff, P.A. & Lima, S.L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. - Trends Ecol. Evol. 13(7): 284–287.

Bertram, B.C.R. (1978). Living in groups: predators and prey. - In: Behavioural Ecology: An Evolutionary Approach (Krebs, J.R. & Davies, N.B. eds.) Oxford: Blackwell Scientific Publications, p. 64–96.

Bertram, B.C.R. (1980). Vigilance and group size in ostriches. - Anim. Behav. 28(1): 278-286.

Bettridge, C.M. & Dunbar, R.I.M. (2012). Predation as a determinant of minimum group size in baboons. - Folia Primatol. 83(3-6): 332-352.

Cameron, E.Z. & du Toit, J.T. (2005). Social influences on vigilance behaviour in giraffes, Giraffa camelopardalis. – Anim. Behav. 69(6): 1337-1344.

Campbell, C.J. (2006). Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). - Am. J. Primatol. 68(12): 1197-1201.

Chance, M.R. (1967). Attention structure as the basis of primate rank orders. - Man 2(4): 503-518.

Cheney, D.L. (1987). Interactions and relationships between groups. – In: Primate societies. (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R. W., & Struhsaker, T.T. eds.) Chicago: University of Chicago Press, p. 227-239.

Childress, M.J. & Lung, M.A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? – Anim. Behav. 66(2): 389-398

Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S. & Manser, M. (1999). Selfish sentinels in cooperative mammals. - Science 284(5420): 1640-1644.

Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys. - Behav. Ecol. Sociobiol. 26(4): 297–300.

Cowlishaw, G. (1998). The role of vigilance in the survival and reproductive strategies of desert baboons. – Behaviour 135(4): 431-452.

Dacier, A., Maia, R., Agustinho, D.P. & Barros, M. (2006). Rapid habituation of scan behavior in captive marmosets following brief predator encounters. – Behav. Process. 71(1): 66-69.

Di Fiore, A. (2002). Predator sensitive foraging in ateline primates. – In: Eat or be Eaten: Predator Sensitive Foraging among Primates (Miller, L.E. ed.). Cambridge University Press, p. 242-267.

Dufour, V., Sueur, C., Whiten, A. & Buchanan-Smith H.M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two New World primates. – Am. J. Primatol. 73(8): 1–10.

Elgar, M.A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence.- Biol. Rev. 64(1): 13-33.

Evers, E., de Vries, H., Spruijt, B.M. & Sterck, E.H. (2012). Look before you leap-individual variation in social vigilance shapes socio-spatial group properties in an agent-based model. - Behav. Ecol. Sociobiol. 66(6): 931-945.

Fairbanks, B. & Dobson, F.S. (2007). Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. – Anim. Behav. 73(1): 115-123.

Fashing, P.J. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. - Behav. Ecol. Sociobiol. 50(3): 219-230.

Favreau, F.R., Goldizen, A.W. & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. - Proc. R. Soc. B. 277(1690): 2089–2095.

Fortin, D., Fortin, M.E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. - Ecology 90(9): 2480-2490.

Foster, W.A. & Treherne, J.E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. – Nature 293: 466-467.

Fraser, O.N., Schino, G. & Aureli, F. (2008). Components of relationship quality in chimpanzees. - Ethology 114(9): 834-843.

Fraser, O.N. & Bugnyar, T. (2010). The quality of social relationships in ravens. – Anim. Behav. 79(4): 927-933.

Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behavior. Cambridge, MA: Harvard University Press.

Hirsch, B.T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). - Behav. Ecol. Sociobiol. 52(6): 458-464.

Hoogland, J.L. & Sherman, P.W. (1976). Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. – Ecol. Monogr. 46(1): 33-58.

Karczmarski, L., Würsig, B., Gailey, G., Larson, K.W. & Vanderlip, C. (2005). Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. - Behav. Ecol. 16(4): 675-685.

Kelley, J.L., Morrell, L.J., Inskip, C., Krause, J. & Croft, D.P. (2011). Predation risk shapes social networks in fission-fusion populations. - PloS One 6(8): 24-28.

Kummer, H. (1971). Primate societies: group techniques of ecological adaptation. Chicago: Aldine.

Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. - Ethology 112(6): 581-591.

Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. – Int. J. Primatol. 28(4): 907-918.

Janson, C.H. (1990). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, Cebus apella. – Anim. Behav. 40(5): 922-934.

Julliot, C. (1994). Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus guianensis*). - Folia Primatol. 63(2): 75-77.

Lazarus, J. (1978). Vigilance, flock size and domain of danger size in the white-fronted goose. - Wild Fowl 29(29): 135–145.

Lazarus, J. (1979). The early warning function of flocking in birds: an experimental study with captive quelea. – Anim. Behav. 27: 855-865.

Lima, S.L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. - Anim. Behav. 49(1): 11–20.

Lung, M.A. & Childress, M.J. (2007). The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. – Behav. Ecol. 18(1): 12-20.

MacIntosh, A.J. & Sicotte, P. (2009). Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): an examination of the effects of conspecific threat and predation. - Am. J. Primatol. 71(11): 919-927.

Matsuda, I. & Izawa, K. **(**2008). Predation of a wild spider monkey at La Macarena, Colombia. - Primates 49(1): 65-68.

McFarland, R., & Majolo, B. (2011). Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). - PLoS One, 6(12):e28826.

McNelis, N.L. & Boatright-Horowitz, S.L. (1998). Social monitoring in a primate group: the relationship between visual attention and hierarchical ranks. – Anim. Cogn. 1(1): 65-69.

Monclús, R. & Rödel, H.G. (2008). Different forms of vigilance in response to the presence of predators and conspecifics in a group - living mammal, the European rabbit. - Ethology 114(3): 287-297.

O’brien, R.M. (2007). A caution regarding rules of thumb for variance inflation factors. – *Qual. Quant. 41*(5): 673-690.

Pays, O., Jarman, P.J., Loisel, P. & Gerard, J.F. (2007). Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? – Anim. Behav. 73(4): 595-604.

Phillips, K.A. (1995). Resource patch size and flexible foraging in white-faced capuchins (*Cebus capucinus*). – Int. J. Primatol. 16(3): 509-520.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2014). R Core Team (2013) nlme: Linear and nonlinear mixed effects models R package version 3.1-117. - URL: http://cran. r-project. org/web/packages/nlme/index. html.

Powell, G.V.N. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. – Anim. Behav. 22(2): 501-505.

Pulliam, H. (1973). On the advantages of flocking. – J. Theor. Biol. 38(2): 419-422.

Quinn, G. & Keough, M. (2002). Experimental Design and Data Analyses for Biologists. Cambridge University Press, New York.

Ramos-Fernandez, G. & Ayala Orozco, B. (2003). Population size and habitat use of spider monkeys at Punta Laguna, Mexico. – In: Primates in Fragments (Marsh L.K. ed.). Kluwer Academic/Plenum Press, New York, p. 191-209.

Ramos-Fernandez, G. (2005). Vocal communication in a fission-fusion society: do spider monkeys stay in touch with close associates? – Int. J. Primatol. 26(5): 1077-1092.

Rebecchini, L., Schaffner, C.M. & Aureli, F. (2011). Risk is a component of social relationships in spider monkeys. - Ethology 117(8): 691-699.

Richards, S.A., Whittingham, M.J. & Stephens, P.A. (2011). Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. - Behav. Ecol. Sociobiol. 65(1): 77–89.

Roberts, G. (1996). Why individual vigilance declines as group size increases. – Anim. Behav. 51(5): 1077–1086.

Rose, L.M. & Fedigan, L.M. (1995). Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. – Anim. Behav. 49(1): 63–70.

de Ruiter, J.R. (1986). The influence of group size on predator scanning and foraging behaviour of wedge capped capuchin monkeys (*Cebus olivaceus*). – Behaviour 98: 240–258.

van Schaik, C.P. (1983). Why are diurnal primates living in groups?. Behaviour 87(1): 120-144.

van Schaik, C.P. & van Hooff, J.A.R.A.M. (1983). On the ultimate causes of primate social systems. – Behaviour 85(1): 91-117.

van Schaik, C.P., van Noordwijk, M.A., Wersono, B. & Sutriono E. (1983). Party size and early detection of predators. - Primates 24(2): 211—221.

Shimooka, Y., Campbell, C.J., Di Fiore, A., Felton, A.M., Izawa, K., Link, A., Nishimura, A., Ramos-Fernandez, G. & Wallace R. (2008): Demography and group composition of *Ateles*. - In: Spider Monkeys: Behavior, Ecology & Evolution of the Genus Ateles (Campbell C. J. ed.). Cambridge University Press, Cambridge, p.329-348

Shopland, J.M. (1982). An intergroup encounter with fatal consequences in yellow baboons (*Papio cynocephalus*). – Am. J. Primatol. 3: 263-266

Sicotte, P. (1993). Intergroup encounters and female transfer in mountain gorillas: Influence of group composition on male behavior. – Am. J Primatol. 30(1): 21-36.

Silk, J.B. (1994). Social relationships of male bonnet macaques: male bonding in a matrilineal society. – Behaviour 130(3): 271-291.

Smith, A.C., Kelez, S. & Buchanan-Smith, H.M. (2004). Factors affecting vigilance within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*). – Behav. Ecol. Sociobiol. 56(1): 18-25.

Stacey, P.B. (1986). Group size and foraging efficiency in yellow baboons. - Behav. Ecol. Sociobiol. 18(3): 1759-187.

Steenbeek, R., Piek, R.C., van Buul, M. & van Hooff J.A. (1999). Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. - Behav. Ecol. Sociobiol. 45(2): 137-150.

Stojan-Dolar, M. & Heymann, E.W. (2010). Vigilance in a cooperatively breeding primate. – Int. J. Primatol. 31(1): 95-116.

Sugiura, H., Saito, C., Sato, S., Agetsuma, N., Takahashi, H., Tanaka, T. & Takahata, Y. (2000). Variation in intergroup encounters in two populations of Japanese macaques. – Int. J. Primatol. 21(3): 519-535.

Symington, M. (1988). Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. – Am. J. Primatol. 15(1): 45–67

Symington, M.M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. - Int. J. Primatol. 11(1): 47-61

Treves, A. (1998). The influence of group size and neighbours on vigilance in two species of arboreal monkeys. – Behaviour 135(4): 453-481.

Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys - Am. J. Primatol. 48(2): 113-126.

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. – Anim. Behav. 60(6): 711–722.

Treves, A., Drescher, A. & Ingrisano, N. (2001). Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). - Behav. Ecol. Sociobiol. 50(1): 90-95.

Valero, A., Schaffner, C.M., Vick, L.G., Aureli, F. & Ramos - Fernandez, G. (2006). Intragroup lethal aggression in wild spider monkeys. - Am. J. Primatol. 68(7): 732-737

van Roosmalen, M.G.M. (1985). Habitat preferences, diet, feeding strategy, and social organization of the black spider monkey (*Ateles p. paniscus* Linnaeus 1758) in Suriname. - Acta Amaz. 15: 1–238.

Wallace, R.B. **(**2008). Towing the party line: territoriality, risky boundaries and male group size in spider monkey fission–fusion societies. – Am. J. Primatol. 70(3): 271-281.

Wilson, M.L. & Wrangham, R.W. (2003). Intergroup relations in chimpanzees. - Ann. Rev. Anthropol. 32: 363–92

Wirtz, P. & Wawra, M. (1986). Vigilance and group size in *Homo sapiens*. - Ethology 71(4): 283–286.

Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. – Ecology 70(1): 164-168.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. - Behaviour 75(3): 262-300.

Captions:

Figure 1: Illustration of the difference in the proportion of time (mean ± SE) spent vigilant depending on the number of neighbours present within 5 m of the focal animal, summarized in four classes.

Figure 2: Illustration of the difference in the proportion of time (mean ± SE) spent vigilant depending on the subgroup size in boundary areas and non-boundary areas.