RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

Vigilance has mainly a social function in a wild group of spider monkeys (*Ateles geoffroyi*)

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Abstract

Vigilance is a widespread behavior that allows individuals to socially acquire information and/or effectively detect potential risks posed by predators and conspecifics. In this study, we aimed to investigate how social factors (i.e., subgroup size, number of males and immatures in the subgroup, presence of fission and fusion events, subgroup activity), individual characteristics (i.e., sex, presence of dependent offspring) and possible vulnerability to predation (i.e., being in smaller subgroups or lower in the canopy) explain variation in vigilance behavior in a wild group of spider monkeys (*Ateles geoffroyi*). We collected vigilance data during focal samples of all adults, subadults and juveniles of the group (*N* = 38), and ran generalized linear mixed models with a Bayesian approach. We found that the proportion of time both sexes spent in vigilance increased with subgroup size and during fusion events. Individuals also spent more time in vigilance when the subgroup was resting or socializing compared to other activities. Moreover, the proportion of time spent in vigilance increased in subgroups with more immatures. An alternative model with similar fit suggested that the proportion of time spent in vigilance increased in females when subgroups included more adult and subadult males. Overall, these results suggest that our study group mainly directed vigilance toward conspecifics (i.e., social vigilance), probably as a result of the relatively low predation pressure experienced, and contribute to the understanding of the multiple social factors affecting vigilance in group-living primates.

KEYWORDS
fission-fusion dynamics, subgroup composition, spider monkeys, vigilance

1 | INTRODUCTION

Vigilance, defined as the behavior of individuals visually monitoring their surroundings beyond their arm's reach, not in the direction of food, is considered a common behavior in several group-living animal species (Treves, 2000). When it does not co-occur with other activities, vigilance may require the allocation of time and attention that individuals have to divert from other activities. Nonetheless, vigilance is thought to provide crucial fitness benefits, by allowing individuals to socially acquire information and by reducing direct

competition, as monitoring others' position and behavior can provide cues about the possible location and value of different resources (Beauchamp, 2001; Schino & Sciarretta, 2016). Moreover, vigilance commonly allows individuals to detect potential risk and anticipate danger (Beauchamp, 2015) and is usually directed to one of two main targets: potential predators (i.e., antipredator vigilance) and conspecifics (i.e., social vigilance).

Antipredator vigilance is aimed at reducing predation risk, and its occurrence may vary depending on the degree of risk faced by individuals. Although larger groups are usually louder and thus easier to be detect by predators than smaller groups, individuals in larger these groups should be *on average* less vigilant than individuals in smaller groups, as they can share antipredator vigilance with other group members (Beauchamp, 2003; Bertram, 1978; Caro, 2005; Roberts, 1996; Treves, 2000; van Schaik & van Hooff, 1983). In birds and mammals, for example, individual vigilance usually is lower in larger groups (Elgar, 1989), although evidence for primates is not as clear (Allan & Hill, 2018; Treves, 2000), possibly because vigilance in primates is often also directed toward conspecifics (Hirsch, 2002; Treves, 1999). Moreover, when the risk is from terrestrial predators, vigilance increases when individuals of arboreal species are lower in the canopy, because they may be more vulnerable to predation (see Isbell, 1994).

Social vigilance is directed to conspecifics, rather than predators, to acquire information from/on others and/or protect individuals from the potential risks that group members or individuals from other groups may pose (e.g., Busia et al., 2019; Kutsukake, 2006; Macintosh & Sicotte, 2009). The proportion of time spent in social vigilance may vary depending on group size, with individuals in larger groups spending more time in social vigilance than individuals in smaller groups if vigilance is mainly directed to other group members (Beauchamp, 2001). Empirical evidence on the link between group size and vigilance is controversial, partly because it is hard to differentiate between vigilance targeting predators and vigilance targeting conspecifics (Allan & Hill, 2018; Beauchamp, 2015). In primates, some studies found that individuals spend less time in vigilance in larger groups (wedge-capped capuchin monkeys, *Cebus olivaceus*: De Ruiter, 1986; common marmosets, *Callithrix jacchus*: Gosselin-Ildari & Koenig, 2012; chacma baboons, *Papio ursinus*: Hill & Cowlishaw, 2002; vervet monkeys, *Chlorocebus pygerythrus*: Isbell & Young, 1993; Japanese macaques, *Macaca fuscata*: Kazahari & Agetsuma, 2010). Other studies, however, found no clear link between vigilance and group size (Geoffroy's spider monkeys, *Ateles geoffroyi*: Busia et al., 2016; chacma baboons: Cowlishaw, 1998; white-faced capuchins, *Cebus capucinus*: Rose & Fedigan, 1995; mustached tamarins, *Saguinus mystax* and saddle-back tamarins, *S. fuscicollis*: Stojan-Dolar & Heymann, 2010; black howler monkeys, *Alouatta pigra*: Treves et al., 2001), or higher individual vigilance levels in larger groups (ursine colobus monkeys, *Colobus vellerosus*: Teichroeb & Sicotte, 2012).

Group size might be a rather imprecise indicator of the risks group members may pose and/or the benefits they may provide. First, vigilance levels may depend on the characteristics of the group members, rather than on their number. In spider monkeys, for instance, the proportion of time spent in vigilance does not generally change with subgroup size, but it increases when the relationship with other subgroup members is insecure (i.e., characterized by high aggression rates and temporal inconsistency in subgroup association), suggesting that social vigilance might be largely directed to monitor conspecifics to reduce potential risks (Busia et al., 2019). Second, vigilance may vary depending on group composition if vigilance is biased to certain categories of group members. To detect potential risks, for example, females might show increased levels of social vigilance as compared to males, especially in the presence of male group members, as females are more likely the target of aggression by males (Campbell, 2003; Fedigan & Baxter, 1984; Klein & Klein, 1977; Link et al., 2009; Slater et al., 2008; Symington, 1987). Similarly, vigilance may depend on the number of immatures or females with dependent offspring, as vigilance is known to be beneficial by increasing immatures' safety (Caro, 2005). Studying how vigilance varies depending on group size and composition, however, is not an easy endeavor, as it generally requires focusing either on several groups or on the same group over an extended period. Comparisons across groups and over time require substantial resources and must address potentially confounding factors, as socio-ecological conditions may differ across groups and time. It might thus be especially effective to focus on species experiencing frequent changes in subgroup size and composition (i.e., having high levels of fission-fusion dynamics; Aureli et al., 2008).

Vigilance might also vary depending on group activity (Cords, 1995; Hirsch, 2002; Kutsukake, 2006; but see Allan & Hill, 2018). Some studies, for instance, reported vigilance to be higher during resting (chacma baboons: Cowlishaw, 1998; Gaynor & Cords, 2012; mustached tamarins, *Saguinus mystax*: Stojan-Dolar & Heymann, 2010; Japanese macaques: Suzuki & Sugiura, 2011), and lower during social interactions (Barbary macaques, *Macaca sylvanus*: Chalmeau et al., 1998; blue monkeys, *Cercopithecus mitis*: Cords, 1995; rhesus macaques, *Macaca mulatta*: Maestripieri, 1993; tamarins: Stojan-Dolar & Heymann, 2010). If groups experience high predation risk, it is possible that vigilance decreases during social interactions because proximity to social partners provides an increased sense of security toward predators, as other group members can be vigilant and/or preyed on (Bertram, 1978; Busia et al., 2016; Delm, 1990; Elgar, 1989; Roberts, 1996; van Schaik & van Hooff, 1983).

Finally, species that are characterized by high levels of fission-fusion dynamics, with frequent changes in subgroup size and composition (Aureli et al., 2008), may face specific challenges that affect their patterns of vigilance. During fission and fusion events, individuals experience important changes in the availability of social partners (Aureli et al., 2008), which might require an increased monitoring of group members. Moreover, individuals cannot witness the interactions between group members that are in other subgroups. During fusion events, therefore, vigilance may be especially significant to rapidly detect changes in such relationships (Aureli et al., 2008; Barrett, 2003).

In this study, we aimed to investigate how different social factors (i.e., subgroup size, number of males and immatures in the subgroup, occurrence of fission and fusion events, subgroup activity), individual characteristics (i.e., sex, presence of dependent offspring) and possible vulnerability to predation (i.e., being in smaller subgroup size and lower in the canopy) may explain variation in the proportion of time spent in vigilance in spider monkeys. Spider monkeys are a good model to study vigilance because they are characterized by high levels of fission-fusion dynamics, with frequent changes in subgroup size and composition (Aureli & Schaffer, 2008). Therefore, it is possible to monitor how the number and type of associating conspecifics (i.e., subgroup size and composition) are linked to changes in vigilance in one single group during a relative short study, and whether fission and fusion events are associated with vigilance patterns.

In spider monkeys, females and immatures are often the target of aggression, especially by males (Aureli & Schaffer, 2008; Campbell, 2003; Fedigan & Baxter, 1984; Link et al., 2009; Slater et al., 2008; Slater et al., 2009; Wallace, 2008), and social vigilance might thus allow females to anticipate the risk that males may pose to them and their dependent offspring. Although predation pressure in the species may be relatively low, and usually limited to few terrestrial predators (Busia et al., 2018; Di Fiore, 2002; Link & Di Fiore, 2013; Link et al., 2011; but see Matsuda & Izawa, 2008), we tested whether vigilance patterns in this species are predicted by the perception of predation risk. If spider monkeys mainly engaged in antipredator vigilance, the proportion of time they spend in vigilance should increase the smaller the subgroup size (Prediction 1) and when lower in the canopy (Prediction 2), as they are more vulnerable to terrestrial predators (Table 1). In contrast, if spider monkeys mainly directed vigilance toward conspecifics, the proportion of time they

engage in vigilance should increase with subgroup size (Prediction 3). Moreover, if spider monkeys use vigilance mainly to prevent potential risks from conspecifics, the proportion of time they engage in vigilance should be higher in females than males (Prediction 4), especially in subgroups including more males (Prediction 5), and in subgroups with more immatures (Prediction 6), in females with dependent offspring (Prediction 7), during fission (Prediction 8) and during fusion events (Prediction 9). Finally, we predict that the proportion of time spider monkeys engage in vigilance would vary depending on subgroup activity (Prediction 10), although we could not make specific predictions due to the inconsistency in previous findings (Allan & Hill, 2018).

2 | METHODS

2.1 | Field site and study subjects

We carried our study in the protected area Otoch Ma'ax Yetel Kooh in Yucatan, Mexico (20° 38' N, 87° 38' W). The protected area includes a mosaic of old-growth, semi-evergreen medium forest and 30–50-year-old successional forest, with patches of younger regenerating forest and lakes (Ramos-Fernández & Ayala-Orozco, 2003). We observed all the individuals belonging to a group of 47 Geoffroy's spider monkeys (*Ateles geoffroyi*), which included 14 adult females, seven adult males, one subadult female, five subadult males, seven juvenile females, two juvenile males, five infant females, and six infant males (see Shimooka et al., 2008 for age categories; Supporting Information: Table S1) when the study started. Group size and composition changed during the study period (from July to

TABLE 1 Predictions, statistical models which better fit to the data and whether the predictions were or not supported (in parentheses, the results of the second set of models, for which the Sex as modulator and the Subgroup composition models provided a similar fit).

Prediction		Set - Model	Supported
If vigilance has mainly an antipredator function, the proportion of time individuals engage in vigilance should increase...			
1	with smaller subgroup size	1 - Predation	No
2	when individuals are lower in the canopy	1 - Predation	No
If vigilance has mainly a social function, the proportion of time individuals engage in vigilance should increase...			
3	with larger subgroup size	1 - Social	Yes
4	in females than males...	1 - Social	No
5	... especially in subgroups containing more males	2 - Sex as modulator	(Yes)
6	in subgroups with more immatures	2 - Subgroup composition	(Yes)
7	in females with dependent offspring	1 - Social	No
8	during fission events	1 - Social	No
9	during fusion events	1 - Social	Yes
In general, the proportion of time they engage in vigilance should vary...			
10	depending on subgroup activity	1 - Social	Yes

December 2021), as two immigrant subadult females joined the group in August 2021 and September 2021, and two infant males were born in November 2021. We could individually recognize all individuals thanks to their facial features and differences in fur coloration, as the study subjects were fully habituated and part of a long-term project (Ramos-Fernandez et al., 2018). We could determine mother-infant dyads through behavioral observations (e.g., nursing) and demographic records collected in previous years, which also allowed us to determine individual age. The study group is characterized by a low predation pressure, with only two predation events having been recorded over 20 years of the long-term study (Busia et al., 2018).

2.2 | Ethics

We obtained permission to conduct the study from CONANP (Comision Nacional de Areas Naturales Protegidas) and SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales). Our study also complied with the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates (ASP, 2001).

2.3 | Data collection

We collected data 5 days a week, from 06:00 to 13:30 from July to December 2021. We used a Cybertracker device (Blackview BV9700 PRO and Runbo F1 4 G 5.5) to conduct 15-min focal animal samples with continuous sampling (Altmann, 1974), with one observer (CBG or SVC) dictating the data to the other who wrote them into the device, which allowed us to record all observable behavior. We started data collection only after the two observers reached 80% interobserver reliability for the coded behaviors (see below). To ensure a similar number of focal samples across subjects, we selected the focal animals on a pseudo-randomized basis (i.e., we prepared a list with all the individuals in a randomized order, and conducted focal observations on the first individual in the list that was present in the subgroup). We did not observe focal animals more than once a day, and we sampled individuals from the same family unit (i.e., mother-offspring, maternal siblings) after at least 30 min from each other. Focal animals were all adults, subadults and juveniles in the group (N = 38) We collected 623 focal samples, resulting in an average of 4.1 h per focal animal.

At the beginning of each focal sample, we recorded subgroup size and composition (i.e., the number and identity of all the individuals within the focal animal's subgroup), and subgroup activity (i.e., whether the activity performed by the majority of visible subgroup members was resting, traveling, feeding, socially interacting or doing other activities; for a description of the recorded behaviors, see (Cant, 1986; Hunt et al., 1996; Lindshield, 2006; van Roosmalen & Klein, 1988). An expert field assistant helped us to keep track of subgroup composition changes. We considered individuals to be part of the focal animal's subgroup, if they were within 30 m from a

subgroup member, using a chain rule (Ramos-Fernández, 2005; cf. Croft et al., 2008). Fission was defined as the departure of one or more individuals from the focal animal's subgroup, when they were not within 30 m of another subgroup member for 30 min (Rebecchini et al., 2011). Fusion was defined as the joining of individuals from different subgroups, when at least one individual of each subgroup come within 30 m of one another (Rebecchini et al., 2011).

During the focal sample, we recorded all visible occurrences of aggression (i.e., lunge, chase, grab, bite) and all fission and fusion events in the subgroup. We further recorded all occurrences of vigilance by the focal animal, and the exact duration spent in vigilance. We defined vigilance as the visual monitoring of the surroundings beyond arm's reach, which was not directed toward food (Busia et al., 2019; Treves, 2000). Specifically, we coded vigilance when the individual had the eyes open, the head up with lifted neck, looking intently usually in a stationary position, and only considered cases in which there was no food in the line of sight of the vigilant individual. A vigilance bout was considered to continue when it was paused for less than 3 s.

We did not attempt to specify the target of vigilance, because it was not possible to determine it with certainty due to the height of the monkeys in the canopy and the dense foliage. As no intergroup encounter occurred during data collection, vigilance was likely not directed to conspecifics other than subgroup members. Every 2 min (starting from the beginning of the focal sample), we further recorded the approximate height of the monkey in the trees (estimated by the observers, after training). We considered monkeys to be more vulnerable to predation when being lower in the canopy, because jaguars and pumas are the main predators of adult spider monkeys (Link & Di Fiore, 2013; Matsuda & Izawa, 2008).

2.4 | Statistical analyses

We ran generalized linear mixed models (Baayen et al., 2008) in R (R Core Team, 2020), using the brms package (version 2.16.3, Bürkner, 2021), which follows a Bayesian approach. We ran two sets of models, each including three different models. In both sets, our response variable was the proportion of time the focal animal spent in vigilance (out of the focal sample duration), which was modeled using a zero-inflated beta distribution. In the first set of models, we entered one line for each focal sample (N = 623). In this set, we compared the fit of three different models: one testing the predictions for antipredator vigilance (Predation model), one testing the predictions for social vigilance (Social model), and one only including controls and random factors (Control model). In the Predation model, we included subgroup size as measured at the beginning of the focal sample (Prediction 1), average canopy height of the focal animal during the focal sample (Prediction 2), and subgroup activity (Prediction 10) as predictor variables. As control variables, we entered whether aggression occurred during the focal sample (0/1) (as vigilance may simply increase after an aggressive event) as a fixed factor, and the identity of the focal animal as a random factor. In the

Social model, we included as predictor variables subgroup size (Prediction 3), the focal animal's sex (Prediction 4), whether the focal animal was a female with dependent offspring (Prediction 7), whether a fission (0/1) or fusion (0/1) event happened during the focal sample (Predictions 8 and 9, respectively), and subgroup activity (Prediction 10). We also included the same control variable and random factor. In the Control model, we only included the control variable and the random factor. Comparing these three models allowed us to assess which set of predictors best explained our data set and thus whether vigilance in our study group mainly served an antipredator function, a social function, or neither of the two.

For the second set of models, we used the same data set, but removed all the focal samples in which fission or fusion events took place during the focal sample, so that the subgroup composition remained the same during the whole focal sample (N = 447). In this second set, we compared the fit of three different models: one testing whether the proportion of time spent in vigilance is affected by subgroup composition depending on the focal animal's sex (Sex as modulator model), one testing whether the proportion of time spent in vigilance is affected by subgroup composition and the focal animal's sex independently (Subgroup composition model), and one only including control variables and random factors (Control model). In the Sex as modulator model, we included the three 2-way interactions of focal animal's sex with number of adult/subadult males (Prediction 5), number of adult/subadult females, and number of immatures in the subgroup (Prediction 6), and the corresponding main terms as predictor variables. We further included the same control variable, random factor and all significant predictors of the first set of models (except for subgroup size, because it was highly correlated with number of adult/subadult males, adult/subadult females and immatures in the subgroup). The Subgroup composition model was identical, except for the absence of the 2-way interactions, although focal animal's sex, number of adult/subadult males, number of adult/subadult females and number of immatures (Prediction 6) in the subgroup were kept as predictor variables. Finally, the Control model only included the control variable, random factor and significant predictors of the first set of models. Comparing these three models allowed us to assess whether the proportion of time spent in vigilance in our study group varied depending on subgroup composition, and whether focal animals' sex modulated this relationship.

Within both sets of models, we compared the three models with the approximate leave-one-out (loo) cross-validation in the loo package, which estimates their pointwise prediction accuracy (Vehtari et al., 2020). We selected the best model depending on the difference (and standard error) between the expected log pointwise predictive densities (elpd) of the models (Vehtari et al., 2017). For categorical predictors (i.e., subgroup activity), we used the emmeans package (v. 1.5.0, Lenth, 2020) to conduct post-hoc comparisons. We ran all models with flat priors, using 4 chains in parallel to increase the number of independent samples from our models and improve inference accuracy, and 2000 iterations for each chain, half of which were warm-up samples to improve sampling

efficiency (McElreath, 2016). We conducted posterior predictive checks using the bayesplot package (Gabry et al., 2019). Convergence was suggested by a high effective number of samples and Rhat estimates of 1.00 (McElreath, 2016). There were no collinearity issues in the models presented (maximum VIFs = 4.77).

3 | RESULTS

For the first set of models, the Predation and the Social models provided a similar fit to the data, and both a better fit than the Control model (elpd ± difference: Predation, 0.0 ± 0.0; Social: −0.8 ± 2.3; Control: −9.6 ± 5.3; Table 2). Inspection of the Predation model, however, revealed that the proportion of time spent in vigilance was higher in larger subgroups, and was not predicted by canopy height (Table 2), in contrast to the predictions that antipredator vigilance should increase with decreasing subgroup size (Prediction 1), and when individuals are lower in the canopy (Prediction 2). The Social model revealed a clear effect of subgroup size, fusion events and subgroup activity on the proportion of time spent in vigilance (Table 2). In particular, the proportion of time spent in vigilance was higher when subgroup size was larger (Table 2; Figure 1), and when fusion events took place during the focal sample (Table 2; Figure 2), supporting Predictions 3 and 9, respectively (Table 1). The odds of engaging in vigilance (i.e., the probability of being vigilant over the probability of not being vigilant) increased by 4% for every additional individual in the subgroup, and by 25% when fusion events occurred. The proportion of time spent in vigilance also varied depending on subgroup activity (Table 2), in line with Prediction 10 (Table 1), being higher during resting and social interactions, as compared to traveling and feeding (post-hoc pairwise comparisons: resting-traveling: β = 0.41, lower-upper 0.95 HPD = 0.09 to 0.74; feeding-resting: β = −0.36, lower-upper 0.95 HPD = −0.57 to −0.15; social interactions-traveling: β = 0.65, lower-upper 0.95 HPD = 0.15 to 1.13; feeding-social interactions: β = −0.60, lower-upper 0.95 HPD = −1.01 to −0.18). We did not find support for Predictions 4, 7, and 8 (Tables 1 and 2).

For the second set of models, the Subgroup composition model provided a slightly better fit to the data than the Sex as modulator model, and a better fit than the Control model (elpd ± difference: Subgroup composition, 0.0 ± 0.0; Sex as modulator: −1.0 ± 3.2; Control: −2.9 ± 3.9; Table 3). Given the relatively low elpd difference between the Subgroup composition and the Sex as modulator models, we present both. The Subgroup composition model revealed that the proportion of time spent in vigilance increased with a higher number of immatures in the subgroup (Table 3), in line with Prediction 6 (Table 1). The odds of engaging in vigilance increased by 9% for every additional immature in the subgroup. The Sex as modulator model revealed an effect of the 2-way interaction between the focal animal's sex and the number of adult/subadult males in the subgroup (Table 3), with a higher number of males leading to an increase in the proportion of time spent in vigilance by females, but not by other males (Figure 3),

TABLE 2 For the first set of models, each predictor of the two best models (Predation and Social models), with reference categories in parentheses, estimate, standard deviation (SD) and two-sided 95% Credible intervals (CIs).

Predictors	Estimate	SD	2.5% to 97.5% CIs
Predation model			
Intercept	−2.24	0.17	−2.58 to −1.90
Subgroup size	0.04	0.01	0.02 to 0.06
Canopy height	0.02	0.02	−0.02 to 0.05
Subgroup activity (other)	0.13	0.61	−1.19 to 1.21
Subgroup activity (resting)	0.31	0.11	0.09 to 0.53
Subgroup activity (social)	0.56	0.21	0.12 to 0.96
Subgroup activity (traveling)	−0.04	0.16	−0.36 to 0.28
Aggressive event	0.08	0.20	−0.31 to 0.46
Social model			
Intercept	−2.20	0.15	−2.49 to −1.91
Subgroup size	0.04	0.01	0.02 to 0.06
Fission event	0.13	0.21	−0.30 to 0.55
Fusion event	0.22	0.11	0.00 to 0.45
Subgroup activity (other)	−0.01	0.65	−1.39 to 1.11
Subgroup activity (resting)	0.36	0.11	0.16 to 0.58
Subgroup activity (social)	0.60	0.21	0.18 to 1.01
Subgroup activity (traveling)	−0.05	0.16	−0.37 to 0.27
Sex (male)	0.07	0.13	−0.19 to 0.33
Female with dependent offspring	−0.05	0.14	−0.33 to 0.23
Aggressive event	0.06	0.20	−0.35 to 0.44

supporting Prediction 5 (Table 1). The odds of engaging in vigilance increased by 16% for every additional adult male in the subgroup.

4 | DISCUSSION

In this study, spider monkeys engaged in vigilance for more time in larger subgroups and when fusion events occurred, depending on subgroup activity and composition, suggesting that vigilance mainly served a social rather than antipredator function. This is in line with literature on spider monkeys suggesting that they experience relatively low predation pressure, usually limited to few terrestrial predators (Busia et al., 2019; Link & Di Fiore, 2013; Link et al., 2011; Matsuda & Izawa, 2008; but see Matsuda & Izawa, 2008). In our study group, predation on spider monkeys has been documented only sporadically by terrestrial predators like pumas (*Puma concolor*; Busia et al., 2018). Moreover, although domestic dogs are present in the area and may sometimes enter
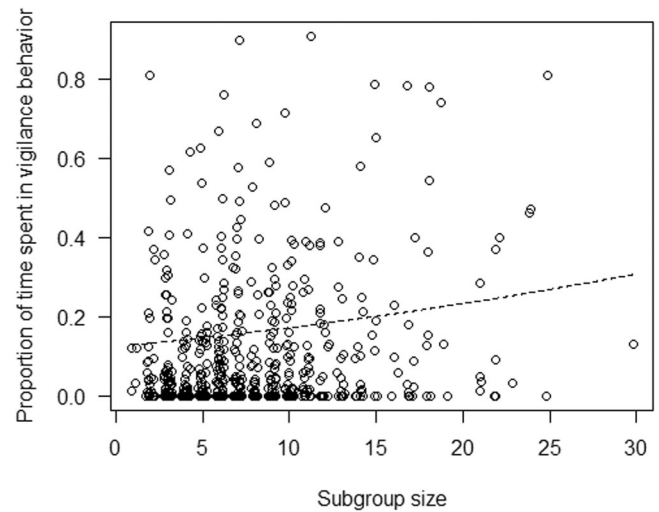

FIGURE 1 Proportion of time spent in vigilance during the focal sample, as a function of subgroup size. Circles represent individual proportions of time for each focal sample, and the line represents the fitted model (Model 1), unconditional on the other predictors that were standardized.
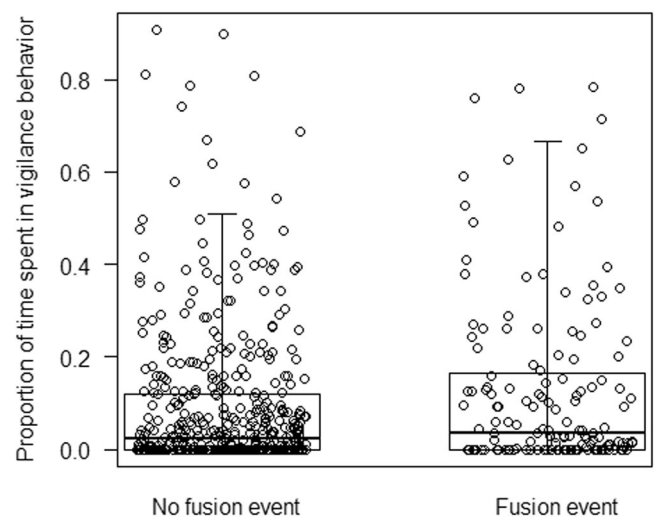

FIGURE 2 Proportion of time spent in vigilance during the focal sample, depending on the occurrence of fusion events. Circles represent individual proportions of time for each focal sample. The thick lines represent the median values for the two conditions, the horizontal ends of the box represent the 75% and 25% quartiles, and the ends of the whiskers represent the 97.5% and 2.5% quartiles.

the forest, they have never been observed predating on the monkeys. During this study, alarm calls were accordingly very scant, as we only recorded eight alarm calls during seven of the 623 focal samples: only in four of these focal samples did the focal subject show vigilance, once in the presence of tourists in the area, and three times in reaction to targets that we could not identify. Therefore, in our study group, vigilance appeared to mainly serve a social function although it may clearly be different at other field sites with higher predation pressure.

TABLE 3 For the second set of models, each predictor of the two best models (Subgroup composition and Sex as modulator models), with reference categories in parentheses, estimate, standard deviation (SD) and two-sided 95% Credible intervals (CIs).

Predictors	Estimate	SD	2.5% to 97.5% CIs
Subgroup composition model			
Intercept	−2.24	0.14	−2.52 to −1.96
Sex (male)	0.18	0.15	−0.13 to 0.48
Number of adult/subadult males in the subgroup	0.04	0.03	−0.02 to 0.09
Number of adult/subadult females in the subgroup	−0.04	0.06	−0.16 to 0.09
Number of immatures in the subgroup	0.09	0.05	0.00 to 0.19
Subgroup activity (other)	0.23	1.26	−2.89 to 2.22
Subgroup activity (resting)	0.27	0.13	0.03 to 0.52
Subgroup activity (social)	0.41	0.25	−0.07 to 0.88
Subgroup activity (traveling)	0.21	0.20	−0.20 to 0.61
Aggressive event	−0.08	0.25	−0.59 to 0.39
Sex as modulator model			
Intercept	−2.16	0.15	−2.47 to −1.87
Number of adult/subadult males in the subgroup * Sex (male)	−0.16	0.06	−0.28 to −0.05
Number of adult/subadult females in the subgroup * Sex (male)	−0.14	0.13	−0.41 to 0.12
Number of immatures in the subgroup * Sex (male)	0.13	0.10	−0.06 to 0.33
Sex (male)	0.27	0.22	−0.16 to 0.70
Number of adult/subadult males in the subgroup	0.15	0.05	0.05 to 0.24
Number of adult/subadult females in the subgroup	0.01	0.07	−0.14 to 0.15
Number of immatures in the subgroup	0.02	0.06	−0.09 to 0.14
Subgroup activity (other)	0.26	1.30	−2.83 to 2.29
Subgroup activity (resting)	0.27	0.12	0.03 to 0.52
Subgroup activity (social)	0.32	0.26	−0.20 to 0.81
Subgroup activity (traveling)	0.16	0.21	−0.27 to 0.56
Aggressive event	−0.14	0.26	−0.67 to 0.34

Individual characteristics of the study subjects had no direct effect on vigilance, although sex modulated the effect of the number of adult males in the subgroup. Vigilance was more common in larger subgroups, in line with Prediction 3 (Table 1) and some previous studies (e.g., Chance, 1967; Hirsch, 2002; Kutsukake, 2006, 2007; McNelis & Boatright-Horowitz, 1998). These results are in line with
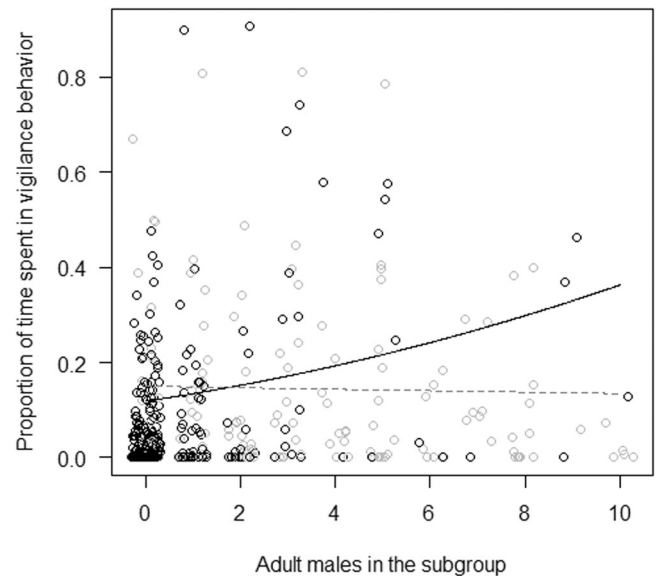

FIGURE 3 Proportion of time spent in vigilance during the focal sample, as a function of number of adult males in the subgroup, separately for female (black) and male (gray) focal animals. Circles represent individual proportions of time for each focal sample (in black, females, and in gray, males), and the lines represents the fitted model (Model 2), unconditional on the other predictors that were standardized (continuous black line for females, dashed gray line for males).

vigilance being used to detect potential risks posed by conspecifics as well as with individuals being vigilant to acquire information from others. The effect of subgroup size seems mainly due to the presence of juveniles and infants, as vigilance levels were higher when a larger number of immatures were in the subgroup (in line with Prediction 6; Table 1), whereas a larger number of adult and subadult males and females had no direct effect on vigilance. These results are thus in line with a previous study on the same group of spider monkeys that found no link between vigilance and subgroup size when the latter was measured based only on the number of adults and subadults in the subgroup (Busia et al., 2016). Possibly, vigilance increases with a larger number of immatures in the subgroup, to protect immatures that face a higher risk of mortality than adults and subadults, mainly due to their smaller size which makes them an easier target for male aggression (Boinski, 1988; Wallace, 2008).

Although we found no overall differences between sexes in terms of vigilance (in contrast to Prediction 4; Table 1), females' vigilance levels, unlike males', were higher when more adult and subadult males were in the subgroup (in line with Prediction 5; Table 1). As females are usually the main target of aggression by adult and subadult males (Campbell, 2003; Fedigan & Baxter, 1984; Klein & Klein, 1977; Link et al., 2009; Slater et al., 2009; Symington, 1987), the presence of adult and subadult males in the subgroup likely enhances females' perception of the risk of being attacked, and thus their vigilance. However, this result should be taken with caution, as the Sex as modulator model in the second set suggests that the modulating effect of sex on vigilance provided a slightly worse fit to

the data than the Subgroup composition model, in which the interaction effect between sex and number of adult and subadult males in the subgroup was not included. Moreover, females in our study also included juvenile females, who might show increased levels of vigilance when approaching sexual maturity (see Alberts, 1994, in baboons).

Our study also showed that vigilance increased when fusion events took place (in line with Prediction 9; Table 1), but not during fission events (in contrast to Prediction 8; Table 1). These findings suggest that mere changes in subgroup composition do not necessarily trigger increased monitoring of conspecifics. However, it is not clear whether the increase in vigilance during fusion events is a byproduct of the increase in subgroup size, or rather reflects the fact that during fusions individuals are exposed to group members with whom they have not interacted for a substantial time (e.g., several hours or days). As predicted, vigilance may thus increase during fusion events to rapidly gather information and detect potential changes in the attitude of joining individuals and the relationships between other group members, which may have occurred when they were in different subgroups (Aureli et al., 2008; Barrett, 2003).

In our study group, vigilance varied depending on subgroup activity, in line with Prediction 10 (Table 1). In particular, vigilance increased when individuals were resting and socially interacting with other group members (i.e., grooming or playing), as compared to traveling and feeding. Previous studies also found an increase in vigilance when individuals were resting (Cowlishaw, 1998; Gaynor & Cords, 2012; Stojan-Dolar & Heymann, 2010; Suzuki & Sugiura, 2011), possibly because individuals have more opportunities to engage in vigilance when they are not involved in demanding activities, such as traveling or foraging. However, in contrast to our study, previous research showed a decrease in vigilance when individuals were engaging in social interactions (e.g., Chalmeau et al., 1998; Cords, 1995; Maestripieri, 1993; Stojan-Dolar & Heymann, 2010). Beyond variation in how variables were operationalized across studies, this difference may also mirror the different functions that vigilance may have across species: when vigilance has mainly a social function, like in our study group, close contact to conspecifics during social interactions may increase vigilance, whereas in species with higher predation, proximity to social partners implies that antipredator vigilance can be shared across group members, so that each individual spends on average less time in vigilance (Delm, 1990; Elgar, 1989; Roberts, 1996; van Schaik & van Hooff, 1983).

Although our study lasted only a few months, we could find predicted effects of several factors on vigilance. It is however possible that we missed subtler effects, and/or factors including seasonal components (e.g., reflecting resource availability and changes in association patterns; Smith-Aguilar et al., 2016; Wallace, 2006), which can only be detected within longer time-frames. Moreover, given the high degree of behavioral diversity primates show within the same species (Strier, 2016; see Santorelli et al., 2011 for *Ateles geoffroyi*), caution must be used in interpreting our results, as we only focused on one study group. In addition, although our study group is characterized by low predation pressure, it is not possible to exclude that some vigilance behavior collected in this study was directed to monitoring predators. In the future, it will be especially important to investigate other aspects of vigilance that we did not address in this study. For instance, it would be interesting to explore the costs that vigilance might imply for animals, by potentially diverting attention and resources from other activities, and specifically test whether spider monkey use social vigilance to acquire information about resources, including the reproductive status of group members. For instance, it is possible that males may be more vigilant in subgroups with more rather than fewer potentially receptive females (although reliance on olfactive cues might be more effective than visual cues), and/or that levels of social vigilance might vary depending on individuals' integration in the social network, with less integrated individuals relying more than other group members on vigilance to detect cues about the location and value of different resources. Our findings overall contribute to the understanding of the multiple co-occurring social factors that explain variation in vigilance across group-living primate species. In particular, our results highlight a variety of social factors that may affect vigilance in species with low predation pressure and complex sociality, characterized by a high degree of fission-fusion dynamics.

CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are attached as Supplementary Materials.

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How to cite this article: Bernardi-Gómez, C., Valdivieso-Cortadella, S., Llorente, M., Aureli, F., & Amici, F. (2023). Vigilance has mainly a social function in a wild group of spider monkeys (*Ateles geoffroyi*). *American Journal of Primatology*, e23559. https://doi.org/10.1002/ajp.23559