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1 **Watch out or relax: conspecifics affect vigilance in wild spider monkeys**2 **(*Ateles geoffroyi*)**3 **Laura Busia<sup>1</sup>, Colleen M. Schaffner<sup>1</sup> & Filippo Aureli<sup>1,2</sup>**4 **<sup>1</sup>Instituto de Neuroetologia, Universidad Veracruzana,**5 **Xalapa, Veracruz, Mexico**6 **<sup>2</sup>Research Centre in Evolutionary Anthropology and Palaeoecology,**7 **Liverpool John Moores University, Liverpool, United Kingdom**

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10

11 **Abstract**

12

13 In most animal species, predation risk is considered the main factor affecting  
14 vigilance, and an individual is expected to spend less time vigilant in larger than  
15 in smaller groups. However, vigilance patterns in primates appear to differ, with  
16 no consistency in group-size effects. As individuals in highly gregarious species  
17 such as diurnal primates face frequent threats from group members, there may  
18 be increased vigilance in larger groups to monitor conspecifics rather than or in  
19 addition to predators. We tested this hypothesis in wild spider monkeys, which  
20 live in communities but fission and fuse in subgroups of variable size and  
21 membership throughout the same day. We found no overall effect of subgroup  
22 size, as traditionally measured, on vigilance. However, a possible explanation is  
23 that vigilance may be effectively shared only with individuals in close proximity,  
24 rather than with all subgroup members. We found that a larger number of  
25 neighbours (i.e., subgroup members within 5m) was associated with a lower

26 proportion of time individuals spent vigilant, which is similar to findings in other  
27 studies. Another social factor that may affect individuals' vigilance is the  
28 possibility of between-community encounters. Higher levels of vigilance can be  
29 expected in areas closer to the boundary of the home range, where between-  
30 community encounters are more likely to occur compared with non-boundary  
31 areas. We found that location in terms of boundary vs. non-boundary areas had  
32 a significant effect on the time individuals spent vigilant in the expected  
33 direction. We also found that location modulated the effect of subgroup size on  
34 vigilance; only in the boundary areas did larger subgroup sizes result in less  
35 individual vigilance time. We concluded that conspecifics affect vigilance of wild  
36 spider monkeys in multiple ways.

37

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

39

## 40 **Introduction**

41

42 Anti-predatory benefits have long been considered a major factor driving group  
43 living (Alexander, 1974; van Schaik, 1983; Elgar, 1989; Roberts, 1996;  
44 Bettridge & Dunbar, 2012). One of the major advantages of group living is  
45 thought to be easier detection of predators in large rather than small groups  
46 ("many-eyes hypothesis" van Schaik & van Hooft, 1983; long-tailed macaques,  
47 *Macaca fascicularis*, van Schaik et al., 1983; Elgar, 1989; dark-eyed  
48 juncos, *Junco hyemalis* and American tree sparrows, *Spizella arborea*, Lima,  
49 1995; Bednekoff & Lima, 1998; meerkats, *Suricata suricata*, Clutton-Brock et  
50 al., 1999, elk, *Cervus elaphus*, Childress & Lung, 2003; Columbian ground

51 squirrels, *Spermophilus columbianus*, Fairbanks & Dobson, 2006), because  
52 there are more individuals that can scan for predators. For example, birds in  
53 larger flocks detect predators sooner and as a result fly away from them from a  
54 larger distance than birds in smaller flocks (starlings, *Sturnus vulgaris*, Powell,  
55 1974; white-fronted geese, *Anser albifrons*, Lazarus, 1978; quelea, *Quelea*  
56 *quelea*, Lazarus, 1979). In an experimental study, the detection of potential  
57 predators occurred earlier in larger than in smaller groups of long-tailed  
58 macaques (van Schaik et al., 1983). In addition, among wild yellow baboons  
59 (*Papio cynocephalus*), individuals in smaller groups stayed closer to large trees  
60 than individuals in larger groups, because of their difficulty in detecting  
61 terrestrial predators, such as lions (*Panthera leo*), leopards (*P. pardus*) and  
62 hyenas (*Crocuta crocuta*) (Stacey, 1986).

63         In vigilance studies, vigilance is defined as the individual monitoring its  
64 surroundings beyond its arm's reach (reviewed in Treves, 2000). Living in large  
65 groups may allow individuals to decrease their own vigilance level without  
66 lessening the group's collective ability to detect predators (Pulliam, 1973; Elgar,  
67 1989; dark-eyed juncos and American tree sparrows, Lima, 1995; Bednekoff &  
68 Lima, 1998; meerkats, Clutton-Brock et al., 1999; elk, Childress & Lung, 2003;  
69 Columbian ground squirrels, Fairbanks & Dobson, 2006). However, across  
70 primate species, researchers often find no association between group size and  
71 individual vigilance (as reviewed by Treves, 2000). This may be because  
72 researchers do not always take into account other factors that might affect the  
73 relationship between group size and vigilance (Elgar, 1989; Treves, 2000;  
74 Beauchamp, 2008). For example, individuals also use vigilance to monitor  
75 conspecifics (Chance, 1967; patas monkey, *Erythrocebus patas*, McNelis &

76 Boatright-Horowitz, 1998; red colobus, *Piliocolobus tephrosceles*, and red-tail  
77 monkey, *Cercopithecus ascanius*, Treves, 1998, 1999, 2000; Evers et al.,  
78 2012). Monitoring conspecifics is useful during the mating season, to avoid  
79 same-sex competitors or to find potential mates (desert baboons, *Papio*  
80 *cynocephalus ursinus*, Cowlishaw, 1998; black howler monkeys, *Alouatta pigra*,  
81 Treves, 1998; see also adult male giraffes, *Giraffa camelopardalis*, Cameron &  
82 du Toit, 2005; adult male elk, Lung & Childress, 2007; European rabbits,  
83 *Oryctolagus cuniculus*, Monclus & Rodel, 2008). Furthermore, within-group  
84 aggression rates are considered higher in primates than in other taxa (Treves,  
85 2000), which may explain why this taxonomic group does not always follow the  
86 expected antipredator patterns for vigilance. Despite the risk of within-group  
87 aggression, individuals in close proximity (hereafter neighbours) do not usually  
88 represent a threat, as individuals that are often neighbours are usually  
89 compatible partners (*sensu* Cords & Aureli, 2000; e.g. bonnet macaques,  
90 *Macaca radiata*, Silk, 1994, chimpanzees, *Pan troglodytes*, Fraser et al., 2008;  
91 ravens, *Corvus corax*, Fraser & Bugnyar, 2010, barbary macaques, *M.*  
92 *sylvanus*, McFarland & Majolo, 2011). Thus, unlike other subgroup members,  
93 neighbours may not require a high degree of monitoring and may even provide  
94 benefits in terms of sharing vigilance. For example, individuals with no close  
95 neighbours were more vigilant than those with at least one neighbour in red  
96 colobus monkey males and red-tail colobus monkey females (Treves, 1998).

97 Another factor affecting vigilance may be the risk posed by conspecifics  
98 from other groups. Between-group relationships in primates are mainly  
99 competitive (Wrangham, 1980) and aggressive or even fatal interactions  
100 between members of different groups have been reported in many primate

101 species (Cheney, 1987; yellow baboons, Shopland, 1982; Japanese macaques  
102 *Macaca fuscata*, Sugiura et al., 2000; black-and-white colobus monkeys,  
103 *Colobus guereza*, Fashing, 2001; mountain gorillas, *Gorilla gorilla*, Sicotte,  
104 1993; chimpanzees, Goodall, 1986; Wilson & Wrangham, 2003). Accordingly,  
105 the time spent vigilant may be higher in areas of the home range where different  
106 groups' home ranges overlap compared to non-overlapping areas, as shown in  
107 Thomas's langurs (*Presbytis thomasi*, Steenbeek et al., 1999) and in black and  
108 white colobus monkeys (Macintosh & Sicotte, 2009).

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

1201.       Given that vigilance is usually considered an anti-predator strategy, few  
121 studies have investigated vigilance in species with low predation pressure.  
122 Thus, little is known about the role of conspecifics on vigilance in species, in  
123 which it is possible to exclude a main role of predation. Spider monkeys  
124 represent an excellent candidate species for several reasons. First, spider  
125 monkeys' high degree of fission-fusion dynamics provides the opportunity to

126 evaluate the effects of the number of associating conspecifics on vigilance as  
127 subgroup size changes frequently throughout the day. Second, there are  
128 relatively few reports of predation events on *Ateles* species (from crested eagle,  
129 *Morphnus guianensis*, Julliot, 1994; jaguar, *Panthera onca*, Matsuda & Izawa,  
130 2008; puma, *Puma concolor*, Di Fiore, 2002; two events involving a puma and  
131 an unidentified terrestrial predator have been recorded in our study site in 18  
132 years: Ramos-Fernandez, pers. comm.; pers. obs.), indicating that their  
133 predation pressure is low. Furthermore, individuals are frequently found alone  
134 or in small subgroups (potentially more vulnerable to predation, Hoogland &  
135 Sherman, 1976; Bertram, 1978; Foster & Treherne, 1981), suggesting predation  
136 pressure has a small role in shaping spider monkey behaviour. Finally, a third  
137 reason spider monkeys are a good model to test the role of conspecifics on  
138 vigilance is because they may be threatened by other communities of the same  
139 species. Spider monkeys are territorial as males patrol their community  
140 boundaries (Wallace, 2008), make incursions into the territory of other  
141 communities (Aureli et al., 2006) and between-community aggressive  
142 encounters have been reported for this taxon (van Roosmalen, 1985;  
143 Symington, 1988).

144         Our aim was to evaluate the role of conspecifics in explaining variation in  
145 spider monkey vigilance. First, we examined whether spider monkey vigilance  
146 was affected by subgroup size. If the hypothesis that vigilance serves mainly to  
147 monitor external threats, such as predators, applies to spider monkeys, we  
148 predicted that individuals would spend less time vigilant in larger than in smaller  
149 subgroups. Alternatively, given that primates face a higher frequency of within-  
150 group aggression compared with other taxa (Treves, 2000) and given that even

151 lethal within-group aggression events have been reported in spider monkeys  
152 (Campbell, 2006; Valero et al., 2006), we predicted that individuals would spend  
153 more time vigilant in larger than in smaller subgroups in order to monitor a  
154 larger number of subgroup members. Second, we evaluated whether the type of  
155 conspecifics affected vigilance. Given that vigilance could be shared with  
156 neighbours (Treves, 1998), we predicted that, regardless of number of animals  
157 in the overall subgroup, the number of neighbours would affect the time spent  
158 vigilant. Third, we examined the role of location in terms of the probability of  
159 between-community encounters. Given that the risk of between-community  
160 encounters is higher at the boundaries of the community home range  
161 (Steenbeek et al., 1999; Macintosh & Sicotte, 2009), we predicted that  
162 individuals would spend more time vigilant at the boundaries of their territory  
163 compared with non-boundary areas. We also predicted that location would play  
164 a modulating role in the relationship between subgroup size and vigilance, as  
165 the collective ability to detect signs of conspecifics from other communities  
166 increases with the number of individuals present in the subgroup.

167

## 168 **Methods**

169

### 170 **Field site and study subjects**

171

172 The field site is located in the forest surrounding the Punta Laguna lake, within  
173 the natural protected area of Otoch Ma'ax Yetel Kooh, Yucatan Peninsula,  
174 Mexico (20°38' N, 87°38' W). The natural protected area measures 5367 ha and  
175 includes a mosaic of old-growth, semi-evergreen medium forest, with trees up

176 to 25 m in height, and 30–50-year-old successional forest (Ramos-Fernandez &  
177 Ayala-Orozco, 2003).

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

189

## 190 **Data collection**

191

192 We observed the monkeys in 4-hour or 8-hour shifts throughout the  
193 course of the day. LB and 2 field assistants followed subgroups (hereafter  
194 subgroup follow) an average of 5.5 hours a day. Data were collecting by using  
195 focal animal sampling (Altmann, 1974). From January to December 2013, 497  
196 15-minute focal samples (mean  $\pm$  SE: 31.1  $\pm$  2.67 per subject; range: 16-50)  
197 were collected by the first author during 750 hours of subgroup follows.

198 During focal samples the time the subject spent vigilant, defined as the  
199 monitoring of the surrounding area beyond arm's reach and not in the direction  
200 of food while foraging (Treves, 2000), was continuously recorded. We also



201 recorded as neighbours all the individuals within 5 m from the focal animal  
202 every two minutes. In addition, we also recorded the time the focal animal was  
203 out of view or the visibility was too poor to reliably observe vigilance. Focal  
204 animals were chosen based on the number of previous focal samples, to have a  
205 similar number of focal samples per individual across the subjects. No animal  
206 was sampled more than once per hour.

207         The subgroup size was continuously updated as we identified every  
208 member of the subgroup initially encountered each day and recorded all  
209 membership changes due to fission and fusion events. An individual was  
210 considered part of the followed subgroup if it was <30 m from a subgroup  
211 member following a chain rule already established for this study site (Ramos-  
212 Fernandez, 2005). Thus, individuals could be spread out over a wide area but  
213 still belong to the same subgroup if they were <30m from at least one subgroup  
214 member. We recorded fission events when one or more individuals were not  
215 seen within 30 m of a subgroup member for 30 minutes. We recorded fusion  
216 events when one or more individuals from a different subgroup came within 30  
217 m from any member of the followed subgroup (Rebecchini et al., 2011). Every  
218 20 minutes we recorded the location of the centre of the subgroup with a  
219 Garmin GPSmap 76Cx.

220

## 221 **Data analyses**

222

223 Linear mixed models (LMMs) were used to examine the effect of several factors  
224 on vigilance. We selected LMMs to allow focal animal identity to be included as  
225 a random factor to account for the lack of independence resulting from multiple

226 focal observations on the same individual. The dependent variable was the  
227 proportion of time the subject spent vigilant in each focal sample. To calculate  
228 this proportion the duration the subject was vigilant was divided by the duration  
229 of the focal sample minus the time the subject was out of view and the time the  
230 visibility was too poor to reliably observe vigilance. We transformed the data  
231 with the arcsine of the square root to normalize them (Quinn & Keough, 2002).  
232 We entered the following independent variables: subgroup size, number of  
233 neighbours and location (boundary or non-boundary areas). Subgroup size was  
234 the number of adults and subadults that were present in the subgroup during  
235 the focal sample; in cases where fission or fusion events occurred during the  
236 focal sample we used the subgroup size occurring for the majority of the focal  
237 sample. The number of neighbours was the mean number of neighbours  
238 present in the 2-minute scans collected during the focal sample. As subgroup  
239 size and number of neighbours are two measures of association between  
240 community members, we evaluated the potential correlation between them and  
241 the Pearson's correlation coefficient was 0.2 (with a low variance inflation factor  
242 of 1.044; O'brien, 2007).

243         In order to classify the location of the focal animal as boundary area or  
244 non-boundary area, we estimated the community home range with GPS data  
245 points using the kernel method (Worton, 1989). We considered the area  
246 between the 80% and the 95% kernel of the utilization distribution as boundary  
247 area and the area within the 80% kernel of the utilization distribution as non-  
248 boundary area. In order to test whether location affected vigilance given the  
249 differential possibility of between-community encounters, we excluded the focal  
250 samples collected at the boundaries along the lake, because no other monkey

251 communities can be present. We also included the interaction between  
252 subgroup size and location as an independent variable. In all analyses, the age  
253 and sex of the focal animal were included in the LMMs as additional  
254 independent variables to control for potentially confounding effects, as well as  
255 the subgroup type (mixed sex or unisex). The best models were chosen using  
256 the lowest Akaike information criteria (AIC, Richards et al., 2011). All the  
257 statistical analyses were carried out using the “nlme” package in R (Pinheiro et  
258 al. 2014). We set an alpha level of  $p < 0.05$  for all tests.

259

## 260 **Results**

261

262 The best model was the full model that included all independent variables (AIC:  
263 -40.27). We found no evidence for subgroup size affecting the proportion of time  
264 individuals spent vigilant (Table 1). In contrast, the number of neighbours had a  
265 statistically significant effect on the proportion of time individuals spent vigilant  
266 (Table 1). A higher number of neighbours was associated with less time spent  
267 vigilant (Figure 1).

268

269 Figure 1 here

270

271 Location also had a significant effect on vigilance: the proportion of time  
272 individuals spent vigilant was higher in boundary (mean  $\pm$  SE:  $0.29 \pm 0.03$ ) than  
273 in non-boundary areas ( $0.27 \pm 0.01$ ; Table 1). In addition, location modulated  
274 the effect of subgroup size on vigilance as there was an effect of the interaction  
275 between subgroup size and location on the proportion of time individuals spent

276 vigilant (Table 1). To better understand the interaction effect, we ran two further  
 277 models, one for each location type. Subgroup size had a significant negative  
 278 relationship with the proportion of time spent vigilant in boundary areas ( $t_{44}=-$   
 279 2.64;  $p=0.01$ , Figure 2), whereas it had no effect in non-boundary areas  
 280 ( $t_{419}=0.84$ ;  $p=0.398$ , Figure 2). Note that large subgroups (9-12 individuals) have  
 281 a smaller sample size than small (1- 4 individuals) and medium subgroups (5- 8  
 282 individuals) and therefore have less weight in the overall means for boundary  
 283 and non- boundary areas.

284

285 Figure 2 here

286

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

	$\beta$	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

289

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

294

## 295 **Discussion**

296

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

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

323           The number of neighbours rather than group size per se seems to be a  
324 factor affecting vigilance. In many studies, a larger number of group members in  
325 proximity was associated with individuals decreasing the proportion of time  
326 spent vigilant (desert baboons, Cowlishaw 1998; Thomas's langurs, Steenbeek  
327 et al., 1999; black howler monkeys, Treves et al., 2001; saddleback tamarins,  
328 *Saguinus fuscicollis*, Smith et al., 2004; moustached tamarins, *S. mystax*, Smith  
329 et al., 2004; Stojan-Dolar & Heymann, 2010; eastern grey kangaroos, *Macropus*  
330 *giganteus*, Favreau et al., 2010). Our findings support the latter relationship.  
331 This could be due to several mechanisms. Antipredator vigilance could be  
332 shared more efficiently among individuals that are in proximity rather than  
333 among all group members, as already shown in red-tail and red colobus  
334 monkeys (Treves, 1998). Individuals may regulate their vigilance according to  
335 the vigilance of other group members (e.g., eastern grey kangaroos, Pays et al.,  
336 2007, Favreau et al., 2010; gulls, *Larus* sp., Beauchamp, 2009) and proximity  
337 may make individuals more aware of their neighbours' activity compared to that  
338 of all subgroup members, thus reducing the need for active monitoring. In

339 addition, the dilution effect might apply more strongly among neighbours than  
340 among all subgroup members (e.g. in white-faced capuchins, Philips, 1995; red  
341 colobus and red-tail monkeys, Treves, 1998). The perception of a lower risk of  
342 predation when individuals have neighbours may lead to lower vigilance levels.  
343 Given the multiple reasons to consider neighbours as an important factor  
344 affecting individual vigilance, it would be prudent to take into account  
345 neighbours in future vigilance studies. Neighbour presence can be thought of as  
346 another association level of individuals (in addition to group size, Treves, 1998).  
347 If not considered, it could represent a confounding factor in the relationship  
348 between vigilance and grouping patterns.

349         As some studies found the presence of neighbours increased the time  
350 individuals spent vigilant (e.g. brown capuchins, Hirsch, 2002; giraffes,  
351 Cameron & du Toit, 2005; chimpanzees: Kutsukake, 2007; elk, Lung &  
352 Childress, 2007; European rabbits, Monclus & Rodel, 2008), the effect of  
353 neighbours on vigilance may be depend on factors such as predation level, the  
354 spatial position within the group, seasonality and social relationships, which  
355 could be evaluated by future comparative research. For example, most  
356 vigilance could be directed to monitoring conspecifics in populations with low  
357 predation risk (Hirsch, 2002). The spatial position within the group may also  
358 play an important role, as central individuals may be less threatened by  
359 predators (e.g. Janson, 1990). In addition, the different effect of neighbours on  
360 vigilance may depend on the season in which the study is conducted. For  
361 example, the increase in male vigilance as the number of neighbours increase  
362 during the breeding season in rabbits may be explained by the need to monitor  
363 conspecifics' activities (Monclus & Rodel 2008). Similarly, the increase in

364 vigilance due to neighbours may be related to reproductive motivation in giraffes  
365 (Cameron & du Toit, 2005). Social relationships may also have a key role in  
366 determining the difference in vigilance depending on the type of neighbours, as  
367 shown in chimpanzees in which an individual was more vigilant when in  
368 proximity with more non-affiliative group members (Kutsukake 2006).

369         Our findings show higher levels of vigilance in boundary compared with  
370 non-boundary areas. This is possibly due to the higher risk of between-  
371 community encounters in boundary areas than in non-boundary areas  
372 (Steenbeek et al., 1999; Macintosh & Sicotte, 2009). The detection of signs of  
373 conspecifics from other communities (e.g. canopy movements) through  
374 vigilance may then reduce the likelihood of hostile between-community  
375 interactions. However, over the years we have witnessed relatively few  
376 between-community encounters involving the study community. Thus, we  
377 exercise caution in our interpretation. An alternative explanation of our findings  
378 may be based on the differential use of the two location types as our boundary  
379 areas are by definition areas included between the 80% and the 95% of the  
380 utilization distribution. It is possible that individuals need to be more vigilant in  
381 areas with a lower degree of use as they are likely less well known and  
382 potentially more risky, as demonstrated for captive black tufted-ear marmosets  
383 (*Callithrix penicillata*, Dacier et al., 2006). This alternative explanation is not,  
384 however, supported by the findings of captive studies in which individuals were  
385 relocated or experimentally located and did not show any significant increase in  
386 vigilance in the novel environment (black tufted-ear marmosets, Barros et al.,  
387 2004; brown capuchin monkeys, *Sapajus apella* and squirrel monkeys, *Saimiri*  
388 *sciureus*, Dufour et al., 2011). Another possible explanation for the difference in



389 vigilance depending on location is that it may be harder for individuals to find  
390 food, which would not be the case in novel environments for captive species  
391 that are fed ad libitum (Barros et al., 2004; Dufour et al., 2011).

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

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

411

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413

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748

749 Captions:

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

753

754 Figure 2: Illustration of the difference in the proportion of time (mean  $\pm$  SE)  
755 spent vigilant depending on the subgroup size in boundary areas and non-  
756 boundary areas.

