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1 Watch out or relax: conspecifics affect vigilance in wild spider monkeys**2 (*Ateles geoffroyi*)****3 Laura Busia¹, Colleen M. Schaffner¹ & Filippo Aureli^{1,2}****4 ¹Instituto de Neuroetologia, Universidad Veracruzana,****5 Xalapa, Veracruz, Mexico****6 ²Research 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 ± 0.03) than
273 in non-boundary areas (0.27 ± 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.

	β	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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424

425

426 **References**

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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.

