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1   **Watch out or relax: conspecifics affect vigilance in wild spider monkeys**

2   **(*Ateles geoffroyi*)**

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

4   **[1]Instituto de Neuroetologia, Universidad Veracruzana,**

5   **Xalapa, Veracruz, Mexico**

6   **[2]Research Centre in Evolutionary Anthropology and Palaeoecology,**

7   **Liverpool John Moores University, Liverpool, United Kingdom**

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10

11   **Abstract**

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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.

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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 Hooff, 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; bisons, *Bison bison*, Fortin et al., 2009; guppies, *Poecilia reticulate,*

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**

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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 ± SE: 31.1 ± 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 ± 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.

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

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

412 **Acknowledgements**

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748

749   Captions:

750   Figure 1: Illustration of the difference in the proportion of time (mean ± 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 ± SE)

755   spent vigilant depending on the subgroup size in boundary areas and non-

756   boundary areas.

757