

**LRH: Asensio, Murillo-Chacon, Schaffner & Aureli**

**RRH:** Effect of roads on spider monkeys

**The effect of roads on spider monkeys' home range and mobility in a heterogeneous regenerating forest**

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1 **ABSTRACT**

2 Arboreal fauna living in tropical ecosystems may be particularly affected by roads given their  
3 dependency on forest cover and the high vulnerability of such ecosystems to changes. Over a  
4 period of four years, we followed subgroups of spider monkeys living in a regenerating dry  
5 tropical forest with 8.2 km of roads within their home range. We aimed to understand whether  
6 roads shaped the home range of spider monkeys and which road features affected their  
7 movement. Only 18 percent (3 km) of the spider monkeys' home range perimeter bordered with  
8 roads; these roads had greater habitat disparity between road sides than roads inside the home  
9 range. Although monkeys were reluctant to be close to roads, and roadside habitat contained low  
10 proportions of mature forest, spider monkeys crossed roads at 69 locations (7.5 crossings per  
11 kilometer). The main road characteristic affecting crossings was canopy opening size, with  
12 greater probability of crossing where canopy openings were smaller. Our findings support the  
13 importance of canopy opening size for road crossing of arboreal taxa, but they also indicate the  
14 relevant role roadside forest structure may have. Minimizing canopy opening size and forest  
15 disturbance along roads can facilitate the movement of arboreal fauna and preserve the important  
16 role of spider monkeys and other arboreal taxa in seed dispersal and thus the maintenance and  
17 regeneration of forest diversity.

18 *Key words:* arboreal mammals, canopy opening, forest structure, Guanacaste Conservation Area,  
19 movement barriers, road crossing, roadside habitat

## 20 INTRODUCTION

21 ROADS ARE WIDESPREAD IN MOST TERRESTRIAL LANDSCAPES AND HAVE AN IMPACT ON THE  
22 ECOSYSTEMS THEY TRAVERSE (Laurance *et al.* 2014). Tropical ecosystems and wildlife therein  
23 are particularly vulnerable to the negative effects associated with road construction and  
24 expansion due to their high vulnerability to environmental changes (Goosem 2007, Laurance *et*  
25 *al.* 2009, Fahrig & Rytwinski 2009). The long-term viability of wildlife metapopulations and  
26 genetic variability depend on the ability of individuals to move freely across the landscape  
27 (Diamond 1975). Therefore, it is critical to understand which road features negatively affect the  
28 movement of different species in order to build or modify roads to minimize their impact on  
29 animal access to critical resources such as food, shelter, mates and potential territories  
30 (Clevenger 2005, Roedenbeck *et al.* 2007).

31 Most studies on the effect of roads on wildlife have focused on terrestrial animals,  
32 whereas research on arboreal species is scarce (but see Asari *et al.* 2010, van der Ree 2010). The  
33 response of arboreal species to roads is likely to differ substantially from that of animals that  
34 travel on the ground. Given their dependence on trees, arboreal species are especially vulnerable  
35 to discontinuities in the habitat created by roads, which add additional obstacles to the physical  
36 challenges already imposed by arboreal locomotion (Asari *et al.* 2010). In addition, roads may  
37 increase the risk of arboreal species being predated when descending to the ground (Fleay 1947,  
38 Zuberbuhler & Jenny 2002). If they do not descend to the ground, arboreal mammals must  
39 negotiate gaps from a reliable support to one that may break, bend, or be unreachable, creating a  
40 falling risk, and thus they may be unable or reluctant to cross canopy openings created by roads  
41 (Wilson *et al.* 2007, Asari *et al.* 2010). Limited suitable road crossing locations may also result  
42 in travel deviation, reducing efficient movement through the canopy (Thorpe *et al.* 2007, Milton

43 2010). However, arboreal mammals have evolved efficient and highly specialized ways of  
44 locomotion to move in an arboreal substrate with the natural discontinuities of the forest canopy  
45 (Jenkins 1974, Cant 1994).

46 The spider monkey (*Ateles* spp.) is a medium size arboreal primate (ca 10 kg) typically  
47 found in the mature tropical forests of Central and South America where most of their habitat has  
48 been encroached and modified for agricultural and urban development (van Roosmalen 1985, Di  
49 Fiore *et al.* 2010). The *Ateles* species tend to disappear from disturbed areas and are especially  
50 sensitive to habitat disturbances (Peres 2001, Ramos-Fernández & Wallace 2008). Spider  
51 monkey populations are declining and all *Ateles* species are considered “Endangered” or  
52 “Critically Endangered” according to the IUCN Red List of Threatened Species (Cuaron *et al.*  
53 2008). In addition, two spider monkey species are regularly listed in the World’s 25 most  
54 endangered primates (Schwitzer *et al.* 2015). Since spider monkeys often inhabit landscapes with  
55 roads and vehicles therein, understanding the impact of roads on spider monkeys is necessary for  
56 their conservation and management.

57 The aim of our study was to investigate the effect of roads on the home range and  
58 mobility of Geoffroy’s spider monkeys (*Ateles geoffroyi*) living in a regenerating dry tropical  
59 forest. First, we examined how roads and characteristics of roadside habitat affected home range  
60 shape. Second, we analyzed road avoidance by spider monkeys by examining the intensity of  
61 spatial use as they approach them. Third, we evaluated spider monkeys’ road crossing behavior  
62 with regard to the characteristics of the roads and roadside habitats. We expected that the greater  
63 the road width, traffic volume, and canopy opening, the more reluctant spider monkeys would be  
64 to cross roads. Similarly, we expected that the presence of cables, disturbed forest at road sides,  
65 as well as asphalt pavement, would hinder spider monkeys’ road crossing.

66

67 **METHODS**

68

69 STUDY SITE. –The study was carried out at the Santa Rosa sector of the Guanacaste Conservation  
70 Area, situated in northwestern Costa Rica (Fig. 1, 10° 50'N, 85° 38'W). The Santa Rosa sector  
71 comprises 108 km<sup>2</sup> of tropical dry forest from the foothills of volcanic mountains down to the  
72 Pacific coastal plain (0–300 m asl) and was originally a large continuous dry forest consisting  
73 mainly of semi-evergreen trees (Janzen 1983, Janzen 1986). However, over the past centuries  
74 much of the upper plateau was cleared by anthropogenic activities (Fedigan & Jack 2001) until  
75 the establishment of a national park in 1971. This history of differential disturbance and  
76 subsequent restoration has resulted in a mosaic landscape with various stages of forest  
77 regeneration, surrounding occasional fragments of old evergreen mature and riparian forest  
78 (Arroyo-Mora *et al.* 2005, De Gama-Blanchet & Fedigan 2006). The Santa Rosa sector has an  
79 internal 7-km paved road that is frequently used to reach a historical site, a camping area, farms,  
80 and the access road to a remote beach and the administrative headquarters of the Guanacaste  
81 Conservation Area from the Pan-American motorway. For example, in 2012 a total of 4960  
82 visitor vehicles used this road (Rodriguez Orozko 2013). This total did not include the several  
83 vehicles of conservation area staff and researchers that circulate on the road on a daily basis The  
84 park is also traversed by a network of secondary dirt roads totaling approximately 20 kilometers

85 Santa Rosa sector consists of a highly seasonal forest with a severe dry season between  
86 December and May and a wet season during the rest of the year when most of the annual rainfall  
87 occurs (900-2500 mm) (Janzen 1986). The habitat types at the study site can be divided into

88 mature forest (*i.e.*, undisturbed old evergreen mature forest, areas of riparian forest or the latest  
89 successional stage forest with an average canopy height of 20 m, Fig. S1), secondary forest (*i.e.*,  
90 deciduous secondary dry forest with an average canopy height of 15 m, Fig. S2), young  
91 secondary forest (*i.e.*, early successional stage deciduous forest with an average canopy height of  
92 5 m, Fig. S3) and no forest (*i.e.*, grasslands and pastures with or without acacia bush layers and  
93 highly scattered trees) (Arroyo-Mora *et al.* 2005, Asensio *et al.* 2012a).

94

95 STUDY SPECIES AND INDIVIDUALS. – Geoffroy's spider monkeys prefer mature forest and  
96 relatively high canopy levels (Chapman 1988, DeGama-Blanchet & Fedigan 2006, Wallace  
97 2008) where higher food density is usually found (Asensio *et al.* 2012a, Ramos Fernandez *et al.*  
98 2013). Spider monkeys are highly arboreal and very rarely venture to the ground with the  
99 exception of particular contexts such as territorial encounters or raids into the home range of  
100 neighboring groups (Campbell *et al.* 2005, Aureli *et al.* 2006). Their agile brachiating and  
101 swinging locomotion is aided by a fully prehensile tail and long limbs (Schmitt *et al.* 2005) that  
102 allow them to perform leaps of up to 5 m when conditions are favorable (Youlatos 2008).

103 The study was carried out between January 2005 and December 2008 for 48 consecutive months.  
104 We studied a community (*i.e.*, a social group) of Geoffroy's spider monkeys that varied in size  
105 (25-34 individuals) over the study period. Monkeys were well habituated to being followed by  
106 researchers and could be individually recognized from pelage and facial patterns as well as sex  
107 and size. This community has the typical grouping pattern of *Ateles* species in which the  
108 community often fissions and fuses into subgroups of different size and composition (Asensio *et*  
109 *al.* 2008). We followed subgroups 3-5 d/wk during the entire course of the daylight hours,

110 balancing observations between mornings and afternoons when whole-day follows were not  
111 possible; observation hours totaled 2691 h (Asensio *et al.* 2012b). We used two procedures to  
112 select the subgroup to follow. First, we randomly selected the subgroup to follow the next day  
113 from the subgroups encountered at the known sleeping sites the night before. Second, we  
114 randomly selected which subgroup to follow after a fission (Asensio *et al.* 2012b).

115

116 HOME RANGE ESTIMATION. –Every 30 min we recorded the location of the followed subgroup  
117 using the track point setting on a handheld global positioning unit (GPS) from roughly the centre  
118 of the subgroup. Geographical coordinates were collected using the coordinate system WGS84  
119 and projected into Universal Transverse Mercator (UTM, Zone 16N) units. A total of 5381 30-  
120 min subgroup location points were collected with a mean ( $\pm$  SD) of 1344 ( $\pm$  301.4) points/yr  
121 (Asensio *et al.* 2015).

122 We used characteristic hull polygons to delineate home range as this method theoretically  
123 best captures the effect of linear barriers on the final boundary shape (Getz *et al.* 2007, Downs &  
124 Horner 2009, Downs *et al.* 2012, Jose-Dominguez *et al.* 2015). Following this method, all 30-  
125 min locations were first connected in a map forming Delaunay triangles of various shapes and  
126 sizes based on their density and spatial distribution (Fig. S4a). The composite of triangles with  
127 perimeters of less than two standard deviations above the mean formed the home range (Fig.  
128 S4b; Downs *et al.* 2012).

129

130 ROAD CHARACTERISTICS. –All roads within the spider monkeys' home range were identified,  
131 georeferenced in a map, their width measured, and their traffic volume estimated based on road

132 surface and accessibility. Thus, a relative high traffic volume was estimated when the road was  
133 paved and had open access all year round, such as the 7-km road from the Pan-American  
134 motorway (Fig. S1 and S2); intermediate traffic volume was estimated in the case of a dirt road  
135 with open access, such as the roads going to the farms inside the Santa Rosa sector; and low  
136 traffic volume was estimated in the case of a dirt road with limited access (Fig. S3), that is, only  
137 all-terrain vehicles authorized by Guanacaste Conservation Area staff were allowed therein. Each  
138 road was divided in 150-m segments (Fig. S5). The pavement type (paved or dirt), presence and  
139 length of electric cable lines running parallel to each road segment were recorded. We also  
140 estimated the proportion of each habitat type (mature forest, medium dry secondary forest, young  
141 dry secondary forest, and no forest) along a 50-m buffer on each side of the road, *i.e.* roadside  
142 habitat types, according to previously published land cover data of the study site (Asensio *et al.*  
143 2012a). We estimated the canopy opening size for each road segment by averaging three canopy  
144 opening measurements, each done every 50 m.

145

146 CHARACTERISTICS OF MONKEYS' CROSSING LOCATIONS. –All locations where spider monkeys  
147 crossed a road were recorded using a GPS (Fig. 1, Fig. S5). We calculated the crossing density as  
148 the number of crossing locations/km for each road segment. For every crossing location we  
149 recorded the width of the road, the pavement type (paved or dirt), the traffic volume (high,  
150 intermediate, low), the presence of cables (yes or no) and the size of the canopy opening between  
151 road sides. To measure the proportion of each habitat type each crossing location was buffered to  
152 a 25 m-radius circle and the proportion of mature forest, medium dry secondary forest, young  
153 dry secondary forest and no forest was determined. For each crossing location a control location  
154 was randomly generated along the same road with the constraint of a minimum distance of 50 m



155 from any crossing location using the “generate random points” tool in ArcGIS (Beyer 2004). The  
156 same measures collected for crossing locations were obtained for control locations.

157

158 DATA ANALYSIS. –All spatial analyses were performed in ArcGIS 10.1 (Environmental Systems  
159 Research Institute, Redlands, USA). We estimated the proportion of the monkeys’ home range  
160 perimeter being affected by roads by creating a buffer of 50 m on each side of the perimeter line  
161 and then calculating the proportion of the buffer zone that included roads. To further understand  
162 the potential effect of roads on home range, we compared the habitat disparity between the two  
163 road sides inside the home range and of roads delimiting home range perimeter. To that aim, we  
164 calculated the proportion of forest habitat, combining mature forest and medium dry secondary  
165 forest in a single category in each 150x50m rectangle at each side of the buffered road segments.  
166 We estimated habitat disparity as the absolute value of the difference in forest habitat proportions  
167 between road sides. A value of habitat disparity close to 0 meant that the forest habitat was  
168 similar on each side of the road, whereas a value close to 1 meant that the forest habitat was  
169 different between road sides. Habitat disparity was compared between the 150-m road segments  
170 along the home range perimeter and the 150-m road segments inside the home range using a *t*-  
171 test. To further understand whether the direction of habitat disparity was due to roads, we also  
172 compared habitat disparity along the home range perimeter between the 150-m segments  
173 overlapping with roads and those that did not. Directional habitat disparity was calculated by  
174 subtracting the proportion of forest habitat in the outer side from that of the inner side of the  
175 home range perimeter. Therefore, values of directional habitat disparity could range from -1,  
176 indicating a higher proportion of forest habitat outside the home range perimeter, to +1,  
177 indicating a higher proportion of forest habitat inside the home range perimeter.

178           Compositional analysis was applied to examine whether roadside habitat types differed  
179 from habitat types available within the home range (Aebischer *et al.* 1993, Conroy & Carroll  
180 2009). Data for this analysis consisted of proportions of each habitat (mature forest, secondary  
181 forest, young secondary forest and no forest) in each buffered road segment compared to  
182 availability in the home range of spider monkeys. Then, the log-ratio difference was calculated  
183 for each habitat pairing relationship using the formula:

$$184 \qquad \qquad \qquad \log - ratio\ difference = \ln \left( \frac{U_1/U_2}{A_1/A_2} \right)$$

185 where  $U_1$  and  $U_2$  are the proportions of two habitat types within a given road segment and  $A_1$   
186 and  $A_2$  the corresponding availability in the home range. A MANOVA with a Wilk's lambda test  
187 was run to determine the statistical significance of the log-ratio differences, which were the  
188 dependent variables, with no independent variables. If the results from the MANOVA were  
189 significant, multiple  $t$ -tests were used to determine whether the log-ratio difference in each  
190 habitat pair category was different from zero, that is, whether the different proportions of habitat  
191 were nonrandom with respect to availability in the home range. The results of the  $t$ -tests were  
192 used to rank the habitat based on the degree of selection or avoidance and to determine which  
193 rankings were significantly different. We ran a second compositional analysis to test whether the  
194 proportions of habitat types in the buffered circles of crossing locations differed from the habitat  
195 types available within the home range. Finally, to understand the habitat preferences at crossing  
196 locations we ran a third compositional analysis to investigate whether the proportions of habitat  
197 types in the buffered circles of crossing locations were different from the proportions of roadside  
198 habitat types.

199 To assess whether spider monkeys avoided roads we buffered each road in 3 parallel  
200 bands at distances to 50, 100, and 150 meters from roads (Fig. S6). Then, we compared the  
201 monkeys' number of locations in each distance band versus the expected frequencies (i.e. the  
202 number of location points in each distance band under an ideal free distribution) between the  
203 three bands with a G test for goodness of fit, with Williams's correction for sample size (Sokal &  
204 Rohlf 1995). An index of road avoidance for each distance band was generated to illustrate  
205 monkey spatial response to road proximity: road avoidance =  $[1 - (\text{observed road}$   
206  $\text{crossings/expected road crossings})] \times 100$  (cf. Laurance *et al.* 2004) with positive values  
207 representing road avoidance and negative values representing attraction to such bands.

208 A generalized linear mixed model (GLMM) fitted for a Poisson distribution was used to  
209 investigate how the number of crossing locations of each road segment (continuous dependent  
210 variable) was affected by the following independent variables: road width, pavement type, traffic  
211 volume, habitat type, segment length with electrical cables and canopy opening. To examine the  
212 factors affecting the likelihood of crossing we used the matching data of crossing control  
213 locations in a GLMM with logit link function with crossing as the binary response variable  
214 (yes/no) and road width, habitat type, presence of cables (yes/no) and canopy opening as the  
215 independent variables. Given that the four habitat type proportions were correlated, we used  
216 principal component analyses (PCA) with varimax rotation to obtain uncorrelated components  
217 that were included as independent variables in both GLMMs. A minimum eigenvalue of 1 was  
218 used to determine the number of components extracted from each PCA. In both GLMMs the  
219 road identity was fitted as a random factor to control for data dependency and between-road  
220 variance. The Akaike information criterion (AIC) was used to select the best explanatory models  
221 (Tabachnick & Fidell 2007). We selected the models with most explanatory support indicated as

222 those within an AIC distance of 2 ( $\Delta AIC \leq 2$ ) and the smallest number of explanatory parameters  
223 (Burnham and Anderson, 2002). Statistical analyses were performed using the statistical  
224 software R (version 3.1.2, R-Core Team, 2013).

225

## 226 **RESULTS**

227

228 **ROAD CHARACTERISTICS.** –The 285-ha home range of spider monkeys was traversed by 16 roads  
229 for a total of 8.2 km in length, 3.9 km of four paved roads and 4.3 km of 12 dirt roads (Fig. 1).  
230 The width of the 16 roads varied from 5 to 7 m (mean $\pm$ SE = 5.1 $\pm$ 0.23, median = 5), and roads  
231 occupied 4.6 hectares of the home range (1.6%). The mean canopy opening along the roads was  
232 3.1 m (SE =  $\pm$ 0.41; N = 64 150-m road segments). The 16,755-m perimeter of the home range  
233 crossed roads in 13 locations. The home range perimeter coincided with roads for a total of 3,016  
234 m and thus bordered roads for 18 percent of its length. The habitat disparity between habitats on  
235 opposing roadsides for roads along this 18 percent home range perimeter was low (mean $\pm$ SE =  
236 0.16 $\pm$ 0.04), but it was significantly greater than that for roads inside the home range (0.07 $\pm$ 0.03;  
237  $t_{56} = 2.1$ ,  $P = 0.04$ ). The proportion of roadside forest habitat was smaller at roads bordering the  
238 home range perimeter (0.59  $\pm$ 0.056) than at roads inside the home range (0.88  $\pm$ 0.02;  $t = 5.48$ ,  $P$   
239 = 0.0003). The home range perimeter bordering roads had higher directional habitat disparity  
240 (0.16 $\pm$ 0.06) than the rest of the home range perimeter not bordering roads (0.05 $\pm$ 0.02;  $t = 2.26$ ,  $P$   
241 = 0.026), indicating that there was a relatively lower proportion of forest habitat in the outer side  
242 of the home range perimeter bordering roads.

243 Roadside habitat mainly consisted of secondary forest (69.9%), followed by young  
244 secondary forest (22.3%), no forest (4.6%), and mature forest (3.2%). Paved and dirt roads had  
245 similar percentages (Chi Square test  $\chi^2 = 4.8$ ,  $p = 0.18$ ) of roadside habitat types (medium dry  
246 secondary forest: 75.1% and 67.8%, young secondary dry forest: 14.3% and 25.4%, no forest  
247 4.7% and 4.5% and mature forest 5.7% and 2.2% for paved and dirt roads, respectively).  
248 Compositional analyses revealed that the proportion of roadside habitat types was not random  
249 with respect to the available habitat in the entire home range (Wilks' lambda,  $\lambda = 0.26$ ,  $P <$   
250  $0.001$ ). The occurrence of secondary forest at roadsides was significantly greater than expected  
251 by its availability in the entire home range compared to that of all the other habitat types,  
252 whereas mature forest was significantly the least represented habitat at roadsides (Table 1).

253 The G test revealed that the number of locations observed across the distance categories  
254 relative to the road, was significantly different from expected by chance both for dirt ( $G = 53.17$ ,  
255  $df = 2$ ,  $P < 0.001$ ) and paved roads ( $G = 180.2$ ,  $df = 2$ ,  $P < 0.001$ ). The results suggest spider  
256 monkey avoidance of the 0-50m distance band while favoring the 101-150m one (Fig. 2). Thus,  
257 proximity to roads increased road avoidance by spider monkeys and altered their movement and  
258 use of the habitat.

259 Considering the 64 150-m road segments within the home range (paved roads = 29; dirt  
260 roads = 35), the mean density of spider monkeys' crossing locations per road was 7.5/km with no  
261 statistical differences between the two types of roads ( $6.9 \pm 1.30$  per km in paved roads and  
262  $8.0 \pm 1.27$  in dirt roads;  $t_{62} = 0.2$ ,  $P = 0.82$ ). Two habitat components were extracted from PCA,  
263 totaling 83.6 percent of overall variance (Table S1). However, the best GLMM explaining the  
264 number of crossings included only the independent variable canopy opening size, which had a  
265 negative effect on crossing density ( $\beta = -0.4$ ,  $SE = 0.1$ ,  $z = -3.93$ ,  $P < 0.001$ ; Fig. 3a).

266

267 CHARACTERISTICS OF CROSSING LOCATIONS. –Spider monkeys were observed to cross roads at 69  
268 locations (30 over paved roads and 39 over dirt roads). Crossing locations were widely  
269 distributed along the road network within the home range of spider monkeys (Fig. 1). Individuals  
270 used tree branches to cross roads in the 69 locations and we never observed them crossing roads  
271 by walking on the ground during the four-year study time. In six locations the monkeys crossed  
272 over the electric cables without touching the wires. Habitat at crossing locations consisted of  
273 mostly secondary forest (60%), followed by young secondary forest (22.5%), mature forest  
274 (10.8%), and no forest (0.6%). Compositional analyses revealed that these proportions differed  
275 from those of the entire home range (Wilks' lambda,  $\lambda = 0.317$ ,  $P < 0.001$ ) and also from those at  
276 roadsides within the home range ( $\lambda = 0.74$ ,  $P < 0.001$ ). In both comparisons the presence of  
277 secondary forest was significantly more likely than that of all the other habitat types at crossing  
278 locations, followed by mature forest, young secondary forest and no forest (Table 1).

279 We included two habitat components extracted with the PCA, totaling 76.7% of the  
280 overall variance (Table S2), into the GLMM. The best GLMM explaining the occurrence of  
281 crossing included the canopy opening and the presence of cables (AIC = 153.5). The canopy  
282 opening had a negative effect on road crossing probability ( $\beta = -0.71$ , SE = 0.16,  $z = -4.3$ ,  $P$   
283  $< 0.001$ ; Fig. 7), whereas crossing probability was higher at road locations with cables ( $\beta = 1.8$ ,  
284 SE = 0.09,  $z = 2.0$ ,  $P = 0.03$ ; Fig. 3b).

285

## 286 **DISCUSSION**

287 We studied the effect of roads on the home range and mobility of a forest-dependent primate  
288 species in a regenerating rainforest. Roads were recurrent features of the home range of the study

289 spider monkeys. Their road-crossing was constrained by canopy opening size, with more  
290 crossings the smaller the opening was. Other road characteristics known to affect negatively  
291 terrestrial animals' movement, such as pavement type or road width, had no effect on spider  
292 monkeys' road crossing. Given that most crossings occurred in secondary forest, which was  
293 abundant at roadsides, this type of forest seems to be structurally adequate for crossing  
294 mitigating the rarity of theoretically more suitable crossing provided by mature forest. Spider  
295 monkeys' road crossing was likely facilitated by their acrobatic locomotion (Schmitt *et al.* 2005,  
296 Youlatos 2008), which can help in coping with moderate adverse conditions (*e.g.*, limited  
297 availability of mature forest at roadsides). Our findings also suggest that roads may structure the  
298 shape of spider monkeys' home range where there is a substantial difference in the habitat  
299 between the two roadsides.

300 Roadside habitat contained a significantly higher proportion of secondary forest and a lower  
301 proportion of mature forest than what expected based on their availability in the home range.  
302 These findings suggest that vegetation along roads in tropical landscapes is subject to edge  
303 effects (Goosem 2007, Laurance *et al.* 2009). However, we do not know whether in the Santa  
304 Rosa sector roads were preferentially built in areas with no mature forest.

305 The spider monkeys' home range perimeter overlapped with roads for 18 percent of its  
306 length. Roads bordering the home range had greater habitat disparity between sides of the road  
307 than did roads inside the home range. Similarly, the habitat disparity was greater in parts of the  
308 home range perimeter that overlapped with roads than in the rest of the perimeter, with a lower  
309 proportion of forest habitat in the outer side of the home range perimeter overlapping with roads  
310 than the rest of the home range perimeter not overlapping with roads. These two differences  
311 together suggest that roads may play a role in structuring the shape of spider monkeys' home

312 range where there is a considerable difference in the habitat between the two roadsides. Given  
313 that roads have a strong effect in creating tropical forest fragments of different size, shape and  
314 degree of isolation (Perz *et al.* 2008), they likely also affect the boundaries of animal home  
315 ranges. Our results support previous findings that animals living in habitats with roads not only  
316 minimize the amount of road in their home range (*e.g.*, *Ursus americanus*, Brody & Pelton 1989;  
317 *Puma concolor*, Dickson & Beier 2002; *Lynx ruffus*, Poessel *et al.* 2014), but they can tolerate  
318 roads depending on the degree of habitat disparity along roadsides.

319 Spider monkeys require large tracts of undisturbed mature forest (Chapman 1988, DeGama-  
320 Blanchet & Fedigan 2006, Wallace 2008). Nevertheless, mature forest did not have a clear effect  
321 on spider monkeys' road crossing probably due to its low availability at roadsides; only 3 percent  
322 of the roadside habitat was composed of mature forest. The limited availability of mature forest  
323 did not however compromise road crossing, as secondary forest, well represented at road sides,  
324 offered sufficient opportunities for spider monkeys to cross roads. Crossing locations were best  
325 predicted by changes in canopy opening size, which was negatively associated with density of  
326 road crossing locations as expected for highly arboreal species such as spider monkeys. Previous  
327 studies on small mammals have similarly found that a narrow canopy opening was a primary  
328 factor favoring road crossings (Asari *et al.* 2010, Ree *et al.* 2010). Spider monkeys can probably  
329 mitigate the negative impact of roads better than other species due to their flexible arboreal  
330 locomotion (Schmitt *et al.* 2005, Youlatos 2008). Other less agile arboreal species at the site,  
331 such as sloths (*Choloepus hoffmanni* and *Bradypus variegatus*) and howler monkeys (*Alouatta*  
332 *palliata*), are likely to be much more constrained by roads than spider monkeys.

333 Unexpectedly, we found that spider monkeys were more likely to cross roads at locations  
334 with electric cables. We need to be cautious about this result as the number of crossing locations



335 with cables in total was very small in our dataset ( $n = 11$ ). In addition, this pattern is unlikely to  
336 be related to spider monkeys' attraction to cables. It is more likely due to electric lines being  
337 clustered in one of the spider monkeys' core areas (Asensio *et al.* 2012b). Cables did not appear  
338 to directly affect crossings because they were under the main canopy at all crossing locations,  
339 and the monkeys used the branches above the cables.

340 Despite the low availability of mature forest at roadsides, and therefore a low number of ideal  
341 crossing locations, spider monkeys did not use some locations with the best characteristics to  
342 cross the road, such as mature forest on both sides and a narrow canopy opening (Fig. 1). This  
343 apparent discrepancy appears to be related to spider monkeys having well-established "arboreal  
344 pathways" or routes that efficiently connect food locations in a relatively large home range (Di  
345 Fiore & Suarez 2007). Because moving away from such routes would be inefficient in terms of  
346 energy employed for travelling (Milton 2000), spider monkeys' movement may not often divert  
347 toward an ideal crossing location if the well-established route allows road crossing, even by  
348 means of some extra effort (*e.g.*, a long jump). Thus, the selection of road crossing locations is  
349 likely a combination of them being situated on a well-established route and containing at least  
350 the minimum adequate characteristics for crossing. This interpretation, along with the high  
351 occurrence of crossing locations in most places of the road network inside the home range,  
352 supports that spider monkeys' movement was not strongly limited by the number of roads within  
353 their home range. However, even if roads may not completely block animal movements, they  
354 could minimize the possible number of routes and hinder the access to areas of the home range  
355 (Merriam *et al.* 1989). For example, during our study a tree branch used by the spider monkeys  
356 to cross the road fell and the monkeys did not use that crossing location again. We could not  
357 fully evaluate whether spider monkeys would have moved differently in the complete absence of

358 roads or whether current crossing locations fully maintain movement connectivity of well-  
359 established routes. However, we found the monkeys to use areas next to roads less often than  
360 expected by chance. This reluctance suggests that spider monkeys tend to approach roads when  
361 necessary for crossing rather than for engaging in foraging, resting or social activities.

362 CONSERVATION AND MANAGEMENT IMPLICATIONS. –Spider monkeys’ reluctance to use areas  
363 close to roads may reduce the benefits derived from their important role as seed dispersers and  
364 “keepers” of forest diversity (Link and Di Fiore 2006). Therefore, our findings highlight the  
365 importance of management road plans and road designs to focus on minimizing canopy opening  
366 size and forest disturbance in order to facilitate their movement. Trees at roads are critical for  
367 the effective movement of spider monkeys and by extension they should be so for other arboreal  
368 fauna as well. However, trees may constitute a risk for drivers as they naturally lose branches or  
369 fall, or trees that fall or grow into electric cables can cause outages and wildfire risk. Thus, even  
370 at national parks under low traffic volumes, managers may feel obligated to cut trees or branches  
371 at roadsides to facilitate driving and reduce hazards. Managing roadside vegetation under this  
372 perception would greatly jeopardize the mobility of spider monkeys and other arboreal species.  
373 A more balanced view that takes into account both human and wildlife perspectives is needed.  
374 After all, the risk of trees causing driving problems or fatalities in a relatively lightly used road  
375 network, such as the study site, is very low (cf. National Tree Safety Group 2001, for evidence of  
376 overall low risk of tree falls to human safety). Tree falls and branches can be promptly removed  
377 from roads, maintaining vehicle mobility safety, such as was witnessed at the study site (pers.  
378 obs). Since spider monkeys use only branches above electric cables to cross roads, managers  
379 could only prune branches and other vegetation that interfere with power lines without affecting  
380 monkeys’ crossing mobility. However, other arboreal fauna may use lower branches to cross the

381 road, and thus it might be more reasonable to replace the overhead lines with underground cables  
382 and minimize cutting trees and tree branches at roads to facilitate arboreal fauna movement.  
383 Nevertheless, if pruning tree branches becomes necessary and compromises the mobility of  
384 arboreal fauna over roads, we suggest piloting the effectiveness of artificial bridging support to  
385 mitigate the potential loss of crossings (e.g. Taylor & Goldingay 2010; Soanes et al. 2015).

386

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388

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397

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577 **Table 1.** Ranking matrices of habitat types at roadsides and crossings compared to the available  
 578 habitat types in the home range of spider monkeys.

<i>Use/availability</i>	Habitats				Rank <sup>a</sup>
	Mature forest	Medium dry secondary forest	Young dry secondary forest	No forest	
<i>Roads/home range</i>					
Mature forest		---	---	---	4
Medium dry secondary forest	+++		+++	+++	1
Young dry secondary forest	+++	---		---	3
No forest	+++	---	+++		2
<i>Crossings/roads</i>					
Mature forest		---	+	+++	2
Medium dry secondary forest	+++		+++	+++	1
Young dry secondary forest	-	---		+++	3
No forest	---	---	---		4
<i>Crossings/home range</i>					
Mature forest		---	+++	+++	2
Medium dry secondary forest	+++		+++	+++	1
Young dry secondary forest	---	---		+	3
No forest	---	---	-		4

579  
 580  
 581  
 582 <sup>a</sup>Relative ranks were determined by counting the number of columns in a row that showed  
 583 greater occurrence with respect to availability of row habitat (Aebischer et al. 1993). Positive  
 584 signs indicate that row habitat was more abundant than column habitat. Negative signs indicate  
 585 that row habitat occurred less than column habitat. Three (positive or negative) signs represent  
 586 significant deviations from random at  $P < 0.05$ , whereas a single sign indicates only a trend.

587 **FIGURE LEGENDS**

588

589 **FIGURE 1.** Location of the study site, roads, and crossing locations (crosses) used by spider  
590 monkeys within their home range. The arrows indicate examples of ideal crossing locations  
591 (mature forest on both sides and narrow canopy opening) that spider monkeys did not use to  
592 cross the road. The cross size is related to the canopy opening size.

593 **FIGURE 2.** Road avoidance index for 0-50m, 51-100m and 101-150m bands of paved and dirt  
594 roads.

595 **FIGURE 3.** Predicted effect ( $\pm 95\%$  confidence intervals) of canopy opening size on the number  
596 of road crossing locations of spider monkeys based on the best generalized linear mixed model  
597 (a). Predicted effect of canopy opening size on the probability of crossing locations with cables  
598 and with no cables based on the best generalized linear mixed model (b).

599

600

601 **SUPPLEMENTARY TABLES**

602

603 **Table S1.** Varimax rotated habitat components from principal component analysis that were  
604 incorporated into the generalized linear mixed model for number of crossings. Values represent  
605 coefficients of correlation between each variable and each component. Values of >0.6 or <-0.6  
606 (marked in bold) were considered high loadings.

<b>Habitat type</b>	<b>Component 1</b>	<b>Component 2</b>
<i>mature forest</i>	<b>-0.956</b>	0.243
<i>medium dry secondary forest</i>	0.197	<b>-0.959</b>
<i>young dry secondary forest</i>	<b>0.796</b>	0.259
<i>no forest</i>	0.478	<b>0.699</b>

607

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610

611 **Table S2.** Varimax rotated habitat components from principal component analysis that were  
612 incorporated into the generalized linear mixed model for occurrence of crossing. Values  
613 represent coefficients of correlation between each variable and each component. Values of >0.6  
614 or <-0.6 (marked in bold) were considered high loadings.

<b>Habitat type</b>	<b>Component 1</b>	<b>Component 2</b>
<i>mature forest</i>	0.151	<b>0.932</b>
<i>medium dry secondary dry forest</i>	<b>-0.961</b>	-0.042
<i>young secondary dry forest</i>	0.445	<b>0.719</b>
<i>no forest</i>	<b>0.723</b>	0.115

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619 **SUPPLEMENTARY FIGURE LEGENDS**

620

621 **FIGURE S1.** A paved road traversing a patch of mature forest habitat at the study site.

622 **FIGURE S2.** A truck entering the study site through the 7-km paved road surrounded by

623 medium secondary dry forest vegetation.

624 **FIGURE S3.** A dirt road traversing a young secondary dry forest at the study site during the dry

625 season.

626 **FIGURE S4.** Steps taken to build home range using all locations (blue dots) the followed

627 subgroup of spider monkeys was every 30 min. First, Delaunay triangles were formed using

628 location points (a). Second, the triangles with perimeters of less than two standard deviations

629 above the mean were used to identify the home range (b).

630

631 **FIGURE S5.** Satellite image (Google TM 2016) showing part of the study site with several

632 types of habitat and a paved road (a) and the same area with rasterized habitat types and

633 vectorized road characteristics (b). Crossing locations are illustrated with crosses and 25-m

634 circular buffers and roads segments of 150x50m are also depicted; cross size is related to the

635 canopy opening size.

636

637 **FIGURE S6.** Example of part of the road with buffered bands at 50, 100 and 150 meters from

638 the road. Locations where the followed subgroup of spider monkeys was every 30 min are

639 represented by blue dots.