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Article

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

INTRODUCTION

ROADS ARE WIDESPREAD IN MOST TERRESTRIAL LANDSCAPES AND HAVE AN IMPACT ON THE

ECOSYSTEMS THEY TRAVERSE (Laurance *et al.* 2014). Tropical ecosystems and wildlife therein

are particularly vulnerable to the negative effects associated with road construction and

expansion due to their high vulnerability to environmental changes (Goosem 2007, Laurance *et*

al. 2009, Fahrig & Rytwinski 2009). The long-term viability of wildlife metapopulations and

genetic variability depend on the ability of individuals to move freely across the landscape

(Diamond 1975). Therefore, it is critical to understand which road features negatively affect the

movement of different species in order to build or modify roads to minimize their impact on

animal access to critical resources such as food, shelter, mates and potential territories

(Clevenger 2005, Roedenbeck *et al.* 2007).

Most studies on the effect of roads on wildlife have focused on terrestrial animals,

whereas research on arboreal species is scarce (but see Asari *et al.* 2010, van der Ree 2010). The

response of arboreal species to roads is likely to differ substantially from that of animals that

travel on the ground. Given their dependence on trees, arboreal species are especially vulnerable

to discontinuities in the habitat created by roads, which add additional obstacles to the physical

challenges already imposed by arboreal locomotion (Asari *et al.* 2010). In addition, roads may

increase the risk of arboreal species being predated when descending to the ground (Fleay 1947,

Zuberbuhler & Jenny 2002). If they do not descend to the ground, arboreal mammals must

negotiate gaps from a reliable support to one that may break, bend, or be unreachable, creating a

falling risk, and thus they may be unable or reluctant to cross canopy openings created by roads

(Wilson *et al.* 2007, Asari *et al.* 2010). Limited suitable road crossing locations may also result

in travel deviation, reducing efficient movement through the canopy (Thorpe *et al.* 2007, Milton

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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.

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METHODS

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STUDY SITE. –The study was carried out at the Santa Rosa sector of the Guanacaste Conservation

Area, situated in northwestern Costa Rica (Fig. 1, 10º 50'N, 85º 38'W). The Santa Rosa sector

comprises 108 km^2 of tropical dry forest from the foothills of volcanic mountains down to the

Pacific coastal plain (0–300 m asl) and was originally a large continuous dry forest consisting

mainly of semi-evergreen trees (Janzen 1983, Janzen 1986). However, over the past centuries

much of the upper plateau was cleared by anthropogenic activities (Fedigan & Jack 2001) until

the establishment of a national park in 1971. This history of differential disturbance and

subsequent restoration has resulted in a mosaic landscape with various stages of forest

regeneration, surrounding occasional fragments of old evergreen mature and riparian forest

(Arroyo-Mora *et al*. 2005, De Gama-Blanchet & Fedigan 2006). The Santa Rosa sector has an

internal 7-km paved road that is frequently used to reach a historical site, a camping area, farms,

and the access road to a remote beach and the administrative headquarters of the Guanacaste

Conservation Area from the Pan-American motorway. For example, in 2012 a total of 4960

visitor vehicles used this road (Rodriguez Orozko 2013). This total did not include the several

vehicles of conservation area staff and researchers that circulate on the road on a daily basis The

park is also traversed by a network of secondary dirt roads totaling approximately 20 kilometers

Santa Rosa sector consists of a highly seasonal forest with a severe dry season between

December and May and a wet season during the rest of the year when most of the annual rainfall

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 (± SD) of 1344 (± 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 el 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
$$log - ratio\ difference = ln\left(\frac{U_1/U_2}{A_1/A_2}\right)$$

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 = $[1 -$ (observed road

206   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

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222   those within an AIC distance of 2 (ΔAIC $\leq$ 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±1.30 per km in paved roads and

262   8.0±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

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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

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

Use/availability	Mature forest	Medium dry secondary forest	Young dry secondary forest	No forest	Rank[a]
Roads/home range					
Mature forest		– – –	– – –	– – –	4
Medium dry secondary forest	+ + +		+ + +	+ + +	1
Young dry secondary forest	+ + +	– – –		– – –	3
No forest	+ + +	– – –	+ + +		2
Crossings/roads					
Mature forest		– – –	+	+ + +	2
Medium dry secondary forest	+ + +		+ + +	+ + +	1
Young dry secondary forest	–	– – –		+ + +	3
No forest	– – –	– – –	– – –		4
Crossings/home range					
Mature forest		– – –	+ + +	+ + +	2
Medium dry secondary forest	+ + +		+ + +	+ + +	1
Young dry secondary forest	– – –	– – –		+	3
No forest	– – –	– – –	–		4

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

FIGURE LEGENDS

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 (±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

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.

Habitat type	Component 1	Component 2
mature forest	**-0.956**	0.243
medium dry secondary forest	0.197	**-0.959**
young dry secondary forest	**0.796**	0.259
no forest	0.478	**0.699**

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.

Habitat type	Component 1	Component 2
mature forest	0.151	**0.932**
medium dry secondary dry forest	**-0.961**	-0.042
young secondary dry forest	0.445	**0.719**
no forest	**0.723**	0.115

615

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618

SUPLEMENTARY 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.