




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

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### ABSTRACT

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

Abstract in Spanish is available with online material.

**Key words:** arboreal mammals; canopy opening; forest structure; Guanacaste Conservation Area; movement barriers; road crossing; roadside habitat.

ROADS ARE WIDESPREAD IN MOST TERRESTRIAL LANDSCAPES AND HAVE AN IMPACT ON THE ECOSYSTEMS THEY TRAVERSE (Benítez-López *et al.* 2010, 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, Fahrig & Rytwinski 2009, Laurance *et al.* 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 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 *et al.* 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, Zuberbühler & 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 (Milton 2000, Thorpe *et al.* 2007). However, arboreal mammals have evolved efficient and highly specialized ways of locomotion to move in an arboreal substrate with the natural discontinuities of the forest canopy (Jenkins 1974, Cant 1994).

The spider monkey (*Ateles* spp.) is a medium size arboreal primate (*ca.* 10 kg) typically found in the mature tropical forests of Central and South America where most of their habitat has been encroached and modified for agricultural and urban development (van Roosmalen 1985, Di Fiore *et al.* 2010). The *Ateles*

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species tend to disappear from disturbed areas and are especially sensitive to habitat disturbances (Peres 2001, Ramos-Fernández & Wallace 2008). Spider monkey populations are declining and all *Ateles* species are considered 'Endangered' or 'Critically Endangered' according to the IUCN Red List of Threatened Species (Cuarón *et al.* 2008). In addition, two spider monkey species are regularly listed in the World's 25 most endangered primates (Schwitzer *et al.* 2015). Since spider monkeys often inhabit landscapes with roads and vehicles therein, understanding the impact of roads on spider monkeys is necessary for their conservation and management.

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

## METHODS

**STUDY SITE.**—The study was carried out at the Santa Rosa sector of the Guanacaste Conservation Area, situated in northwestern Costa Rica (Fig. 1, 10°50' N, 85°38' W). The Santa Rosa sector comprises 108 km<sup>2</sup> 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, 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 (Rodríguez 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 approx. 20 km.

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

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

The study was carried out between January 2005 and December 2008 for 48 consecutive months. We studied a community (*i.e.*, a social group) of Geoffroy's spider monkeys that varied in size (25–34 individuals) over the study period. Monkeys were well habituated to being followed by researchers and could be individually recognized from pelage and facial patterns as well as sex and size. This community has the typical grouping pattern of *Ateles* species in which the community often fissions and fuses into subgroups of different size and composition (Asensio *et al.* 2008). We followed subgroups 3–5 d/wk during the entire course of the daylight hours, balancing observations between mornings and afternoons when whole-day follows were not possible; observation hours totaled 2691 h (Asensio *et al.* 2012b). We used two procedures to select the subgroup to follow. First, we randomly selected the subgroup to follow the next day from the subgroups encountered at the known sleeping sites the night before. Second, we randomly selected which subgroup to follow after a fission (Asensio *et al.* 2012b).

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

We used characteristic hull polygons to delineate home range as this method theoretically best captures the effect of linear barriers on the final boundary shape (Getz *et al.* 2007, Downs & Horner 2009, Downs *et al.* 2012, José-Domínguez *et al.* 2015). Following this method, all 30-min locations were first connected in a map forming Delaunay triangles of various shapes and sizes

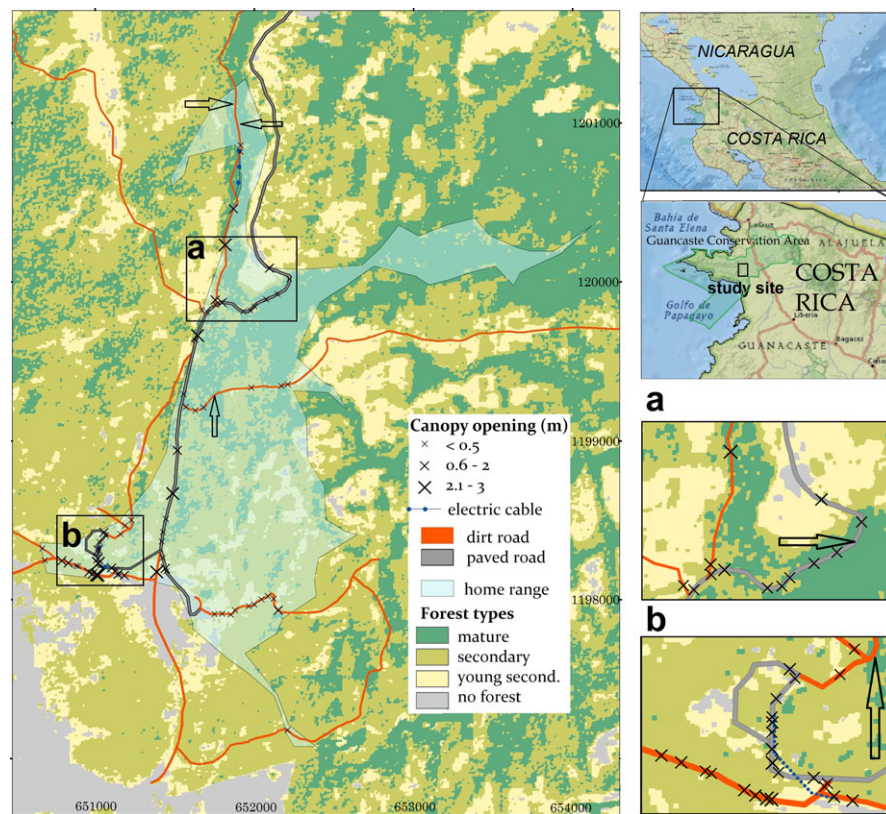


FIGURE 1. Location of the study site, roads, and crossing locations (crosses) used by spider monkeys within their home range. The arrows indicate examples of ideal crossing locations (mature forest on both sides and narrow canopy opening) that spider monkeys did not use to cross the road. The cross-size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

based on their density and spatial distribution (Fig. S4A). The composite of triangles with perimeters of less than two standard deviations above the mean formed the home range (Fig. S4B; Downs *et al.* 2012).

**ROAD CHARACTERISTICS.**—All roads within the spider monkeys' home range were identified, georeferenced in a map, their width measured, and their traffic volume estimated based on road surface and accessibility. Thus, a relative high traffic volume was estimated when the road was paved and had open access all year round, such as the 7-km road from the Pan-American motorway (Figs. S1 and S2); intermediate traffic volume was estimated in the case of a dirt road with open access, such as the roads going to the farms inside the Santa Rosa sector; and low traffic volume was estimated in the case of a dirt road with limited access (Fig. S3), that is, only all-terrain vehicles authorized by Guanacaste Conservation Area staff were allowed therein. Each road was divided into 150-m segments (Fig. S5). The pavement type (paved or dirt), presence and length of electric cable lines running parallel to each road segment were recorded. We also estimated the proportion of each habitat type (mature forest, medium dry secondary forest, young dry secondary forest, and no forest) along a 50-m buffer on each side of the road, *i.e.*, roadside habitat types, according to previously published land cover data of

the study site (Asensio *et al.* 2012a). We estimated the canopy opening size for each road segment by averaging three canopy opening measurements, each done every 50 m.

**CHARACTERISTICS OF MONKEYS' CROSSING LOCATIONS.**—All locations where spider monkeys crossed a road were recorded using a GPS (Figs. 1 and S5). We calculated the crossing density as the number of crossing locations/km for each road segment. For every crossing location, we recorded the width of the road, the pavement type (paved or dirt), the traffic volume (high, intermediate, low), the presence of cables (yes or no), and the size of the canopy opening between road sides. To measure the proportion of each habitat type each crossing location was buffered to a 25 m-radius circle and the proportion of mature forest, medium dry secondary forest, young dry secondary forest, and no forest was determined. For each crossing location, a control location was randomly generated along the same road with the constraint of a minimum distance of 50 m from any crossing location using the 'generate random points' tool in ArcGIS (Beyer 2004). The same measures collected for crossing locations were obtained for control locations.

**DATA ANALYSIS.**—All spatial analyses were performed in ArcGIS 10.1 (Environmental Systems Research Institute, Redlands,



California, U.S.A.). We estimated the proportion of the monkeys' home range perimeter being affected by roads by creating a buffer of 50 m on each side of the perimeter line and then calculating the proportion of the buffer zone that included roads. To further understand the potential effect of roads on home range, we compared the habitat disparity between the two road sides inside the home range and of roads delimiting home range perimeter. To that aim, we calculated the proportion of forest habitat, combining mature forest and medium dry secondary forest in a single category in each  $150 \times 50$  m rectangle at each side of the buffered road segments. We estimated habitat disparity as the absolute value of the difference in forest habitat proportions between road sides. A value of habitat disparity close to 0 meant that the forest habitat was similar on each side of the road, whereas a value close to 1 meant that the forest habitat was different between road sides. Habitat disparity was compared between the 150-m road segments along the home range perimeter and the 150-m road segments inside the home range using a *t*-test. To further understand whether the direction of habitat disparity was due to roads, we also compared habitat disparity along the home range perimeter between the 150-m segments overlapping with roads and those that did not. Directional habitat disparity was calculated by subtracting the proportion of forest habitat in the outer side from that of the inner side of the home range perimeter. Therefore, values of directional habitat disparity could range from  $-1$ , indicating a higher proportion of forest habitat outside the home range perimeter, to  $+1$ , indicating a higher proportion of forest habitat inside the home range perimeter.

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

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

where  $U_1$  and  $U_2$  are the proportions of two habitat types within a given road segment and  $A_1$  and  $A_2$  the corresponding availability in the home range. A MANOVA with a Wilk's lambda test was run to determine the statistical significance of the log-ratio differences, which were the dependent variables, with no independent variables. If the results from the MANOVA were significant, multiple *t*-tests were used to determine whether the log-ratio difference in each habitat pair category was different from zero, that is, whether the different proportions of habitat were nonrandom with respect to availability in the home range. The results of the *t*-tests were used to rank the habitat based on the degree of selection or avoidance and to determine which rankings were significantly different. We ran a second compositional analysis to test

whether the proportions of habitat types in the buffered circles of crossing locations differed from the habitat types available within the home range. Finally, to understand the habitat preferences at crossing locations, we ran a third compositional analysis to investigate whether the proportions of habitat types in the buffered circles of crossing locations were different from the proportions of roadside habitat types.

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

A generalized linear mixed model (GLMM) fitted for a Poisson distribution was used to investigate how the number of crossing locations of each road segment (continuous dependent variable) was affected by the following independent variables: road width, pavement type, traffic volume, habitat type, segment length with electrical cables and canopy opening. To examine the factors affecting the likelihood of crossing, we used the matching data of crossing control locations in a GLMM with logit link function with crossing as the binary response variable (yes/no) and road width, habitat type, presence of cables (yes/no), and canopy opening as the independent variables. Given that the four habitat type proportions were correlated, we used principal component analyses (PCA) with varimax rotation to obtain uncorrelated components that were included as independent variables in both GLMMs. A minimum eigenvalue of 1 was used to determine the number of components extracted from each PCA. In both GLMMs, the road identity was fitted as a random factor to control for data dependency and between-road variance. The Akaike information criterion (AIC) was used to select the best explanatory models (Tabachnick & Fidell 2007). We selected the models with most explanatory support indicated as those within an AIC distance of 2 ( $\Delta\text{AIC} \leq 2$ ) and the smallest number of explanatory parameters (Burnham & Anderson 2002). Statistical analyses were performed using the statistical software R (v. 3.1.2, R-Core Team 2013).

## RESULTS

**ROAD CHARACTERISTICS.**—The 285-ha home range of spider monkeys was traversed by 16 roads 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). The width of the 16 roads varied from 5 to 7 m (mean  $\pm$  SE =  $5.1 \pm 0.23$ , median = 5), and roads occupied 4.6 hectares of the home range (1.6%). The mean canopy opening along the roads was 3.1 m (SE =  $\pm 0.41$ ;  $N = 64,150$ -m road

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	Habitats				Rank <sup>a</sup>
	Mature forest	Medium dry secondary forest	Young dry secondary forest	No forest	
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

<sup>a</sup>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.

segments). The 16,755-m perimeter of the home range crossed roads in 13 locations. The home range perimeter coincided with roads for a total of 3016 m and thus bordered roads for 18 percent of its length. The habitat disparity between habitats on opposing roadsides for roads along this 18 percent home range perimeter was low (mean  $\pm$  SE =  $0.16 \pm 0.04$ ), but it was significantly greater than that for roads inside the home range ( $0.07 \pm 0.03$ ;  $t_{56} = 2.1$ ,  $P = 0.04$ ). The proportion of roadside forest habitat was smaller at roads bordering the home range perimeter ( $0.59 \pm 0.056$ ) than at roads inside the home range ( $0.88 \pm 0.02$ ;  $t = 5.48$ ,  $P = 0.0003$ ). The home range perimeter bordering roads had higher directional habitat disparity ( $0.16 \pm 0.06$ ) than the rest of the home range perimeter not bordering roads ( $0.05 \pm 0.02$ ;  $t = 2.26$ ,  $P = 0.026$ ), indicating that there was a relatively lower proportion of forest habitat in the outer side of the home range perimeter bordering roads.

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

types, whereas mature forest was significantly the least represented habitat at roadsides (Table 1).

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

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

**CHARACTERISTICS OF CROSSING LOCATIONS.**—Spider monkeys were observed to cross-roads at 69 locations (30 over paved roads and 39 over dirt roads). Crossing locations were widely distributed along the road network within the home range of spider monkeys (Fig. 1). Individuals used tree branches to cross-roads in the 69 locations and we never observed them crossing roads by walking

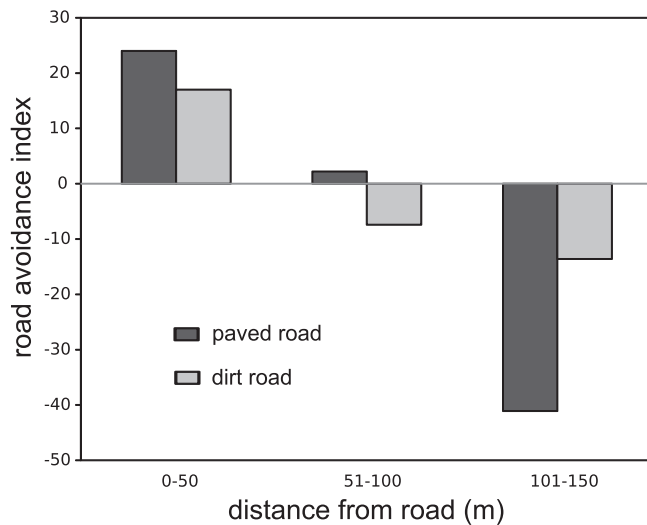


FIGURE 2. Road avoidance index for 0–50 m, 51–100 m, and 101–150 m bands of paved and dirt roads.

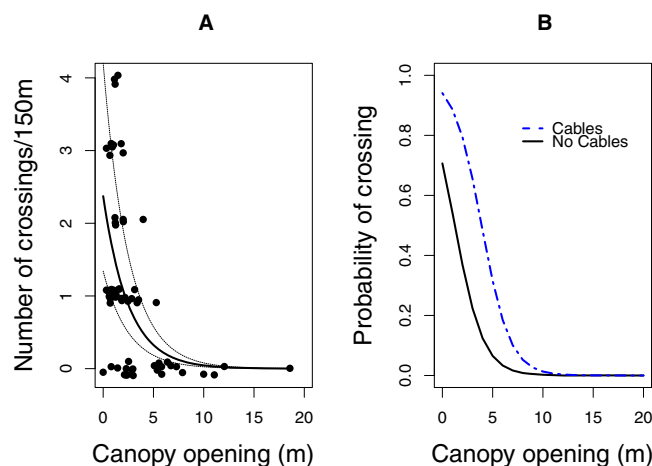


FIGURE 3. (A) Predicted effect ( $\pm 95\%$  confidence intervals) of canopy opening size on the number of road crossing locations of spider monkeys based on the best generalized linear mixed model. (B) Predicted effect of canopy opening size on the probability of crossing locations with cables and with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

on the ground during the 4-year study time. In six locations, the monkeys crossed over the electric cables without touching the wires. Habitat at crossing locations consisted of mostly secondary forest (60%), followed by young secondary forest (22.5%), mature forest (10.8%), and no forest (0.6%). Compositional analyses revealed that these proportions differed from those of the entire home range (Wilks' lambda,  $\lambda = 0.317$ ,  $P < 0.001$ ) and also from those at roadsides within the home range ( $\lambda = 0.74$ ,  $P < 0.001$ ). In both comparisons, the presence of secondary forest was significantly more likely than that of all the other habitat types at crossing locations, followed by mature forest, young secondary forest and no forest (Table 1).

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

## DISCUSSION

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

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

The spider monkeys' home range perimeter overlapped with roads for 18 percent of its length. Roads bordering the home range had greater habitat disparity between sides of the road than did roads inside the home range. Similarly, the habitat disparity was greater in parts of the home range perimeter that overlapped with roads than in the rest of the perimeter, with a lower proportion of forest habitat in the outer side of the home range perimeter overlapping with roads than the rest of the home range perimeter not overlapping with roads. These two differences together suggest that roads may play a role in structuring the shape of spider monkeys' home range, where there is a considerable difference in the habitat between the two roadsides. Given that roads have a strong effect in creating tropical forest fragments of different size, shape, and degree of isolation (Perz *et al.* 2008), they likely also affect the boundaries of animal home ranges. Our results support previous findings that animals living in habitats with roads not only minimize the amount of road in

their home range (e.g., *Ursus americanus*, Brody & Pelton 1989, *Puma concolor*, Dickson & Beier 2002, *Lynx rufus*, Poessel *et al.* 2014), but they can tolerate roads depending on the degree of habitat disparity along roadsides.

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

Unexpectedly, we found that spider monkeys were more likely to cross roads at locations with electric cables. We need to be cautious about this result as the number of crossing locations with cables in total was very small in our dataset ( $N = 11$ ). In addition, this pattern is unlikely to be related to spider monkeys' attraction to cables. It is more likely due to electric lines being clustered in one of the spider monkeys' core areas (Asensio *et al.* 2012b). Cables did not appear to directly affect crossings because they were under the main canopy at all crossing locations, and the monkeys used the branches above the cables.

Despite the low availability of mature forest at roadsides, and therefore a low number of ideal crossing locations, spider monkeys did not use some locations with the best characteristics to cross the road, such as mature forest on both sides and a narrow canopy opening (Fig. 1). This apparent discrepancy appears to be related to spider monkeys having well-established 'arboreal pathways' or routes that efficiently connect food locations in a relatively large home range (Di Fiore & Suarez 2007). Because moving away from such routes would be inefficient in terms of energy employed for traveling (Milton 2000), spider monkeys' movement may not often divert toward an ideal crossing location if the well-established route allows road crossing, even by means of some extra effort (e.g., a long jump). Thus, the selection of road crossing locations is likely a combination of them being situated on a well-established route and containing at least the minimum adequate characteristics for crossing. This interpretation, along with the high occurrence of crossing locations in most places of the road network inside the home range, supports that spider monkeys' movement was not strongly limited by the number of roads within their home range. However, even if roads

may not completely block animal movements, they could minimize the possible number of routes and hinder the access to areas of the home range (Merriam *et al.* 1989). For example, during our study a tree branch used by the spider monkeys to cross the road fell and the monkeys did not use that crossing location again. We could not fully evaluate whether spider monkeys would have moved differently in the complete absence of roads or whether current crossing locations fully maintain movement connectivity of well-established routes. However, we found the monkeys to use areas next to roads less often than expected by chance. This reluctance suggests that spider monkeys tend to approach roads when necessary for crossing rather than for engaging in foraging, resting or social activities.

**CONSERVATION AND MANAGEMENT IMPLICATIONS.**—Spider monkeys' reluctance to use areas close to roads may reduce the benefits derived from their important role as seed dispersers and 'keepers' of forest diversity (Link & Di Fiore 2006). Therefore, our findings highlight the importance of management road plans and road designs to focus on minimizing canopy opening size and forest disturbance to facilitate their movement. Trees at roads are critical for the effective movement of spider monkeys and by extension they should be so for other arboreal fauna as well. However, trees may constitute a risk for drivers as they naturally lose branches or fall, or trees that fall or grow into electric cables can cause outages and wildfire risk. Thus, even at national parks under low traffic volumes, managers may feel obligated to cut trees or branches at roadsides to facilitate driving and reduce hazards. Managing roadside vegetation under this perception would greatly jeopardize the mobility of spider monkeys and other arboreal species. A more balanced view that takes into account both human and wildlife perspectives is needed. After all, the risk of trees causing driving problems or fatalities in a relatively lightly used road network, such as the study site, is very low (cf. National Tree Safety Group 2011, for evidence of overall low risk of treefalls to human safety). Treefalls and branches can be promptly removed from roads, maintaining vehicle mobility safety, such as was witnessed at the study site (pers. obs). Since spider monkeys use only branches above electric cables to cross-roads, managers could only prune branches and other vegetation that interfere with power lines without affecting monkeys' crossing mobility. However, other arboreal fauna may use lower branches to cross the road, and thus it might be more reasonable to replace the overhead lines with underground cables and minimize cutting trees and tree branches at roads to facilitate arboreal fauna movement. Nevertheless, if pruning tree branches becomes necessary and compromises the mobility of arboreal fauna over roads, we suggest piloting the effectiveness of artificial bridging support to mitigate the potential loss of crossings (e.g., Taylor & Goldingay 2012, Soanes *et al.* 2015).

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## DATA AVAILABILITY

Data deposited in the Dryad Repository: <https://doi.org/10.5061/dryad.pt240> (Asensio *et al.* 2017).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Varimax rotated habitat components from principal component analysis that were incorporated into the generalized linear mixed model for number of crossings.*

TABLE S2. *Varimax rotated habitat components from principal component analysis that were incorporated into the generalized linear mixed model for occurrence of crossing.*

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

FIGURE S2. A truck entering the study site through the 7-km paved road surrounded by medium secondary dry forest vegetation.

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

FIGURE S4. Steps taken to build home range using all locations.

FIGURE S5. Satellite image showing part of the study site with several types of habitat and a paved road and the same area with rasterized habitat types and vectorized road characteristics.

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

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