Anthropogenic habitat disturbance and food availability affect the abundance of an endangered primate: a regional approach

Denise Spaan[a,b,c], Gabriel Ramos-Fernández[b,d,e], Martha Bonilla-Moheno[f], Colleen M. Schaffner[b,g], Jorge E. Morales-Mávil[a], Kathy Slater[h] and Filippo Aureli[a,b,i]

a. Instituto de Neuroetología, Universidad Veracruzana, Avenida Dr. Luis Castelazo s/n, Xalapa, 91190 Veracruz, Mexico. dspaan@uv.mx, jormorales@uv.mx, faureli@uv.mx
b. ConMonoMaya, A.C., Km 5.4 carretera Chemax-Coba, Chemax, 97770 Yucatan, Mexico.
c. Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Avenida Juanito Itzicuaro, Morelia, 58330 Michoacan, Mexico.
d. Instituto de Investigaciones en Matemáticas Aplicadas y en Sistemas, Universidad Nacional Autónoma de Mexico, Circuto Escolar 3000, C.U., 04510, Mexico City, Mexico. ramosfer@alumni.upenn.edu
e. Unidad Interdisciplinaria en Ingeniería y Tecnologías Avanzadas, Instituto Politécnico Nacional, Av Instituto Politécnico Nacional 2580, La Laguna Ticoman, 07340, Mexico City, Mexico.
f. Red de Ambiente y Sustentabilidad, Instituto de Ecología A.C., Carretera antigua a Coatepec 351, El Haya, Xalapa 91073, Veracruz, México. martha.bonilla@inecol.mx
g. Psychology Department, Adams State University, 208 Edgemont Blvd, Alamosa, CO 81101, USA. cschaffner@adams.edu
h. Research Department, Operation Wallacea, Old Bolingbroke, Spilsby, Lincolnshire PE23 4EX, United Kingdom. kathy.slater@opwall.ac.uk
i. Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Byron Street, Liverpool L3 3AF, United Kingdom.

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Corresponding author:
Denise Spaan
Instituto de Neuroetología, Universidad Veracruzana, Av. Dr. Luis Castelazo s/n, Col. Industrial Animas, Xalapa, Veracruz 91190, Mexico.
dspaan@uv.mx

ABSTRACT

Anthropogenic habitat disturbances are causing large-scale declines in animal abundance. For many species, information on the drivers of decline is lacking or restricted to single sites, despite calls for regional approaches. In this study, we determined the effect of different types of habitat disturbance (natural or anthropogenic) and ecological factors on Geoffroy's spider monkey (*Ateles geoffroyi*) abundance using a regional approach. We selected this study species because of its high degree of social flexibility and its endangered status. We surveyed 4 sites in the Yucatan Peninsula and recorded the number of individual monkeys encountered along 72 line-transect segments each measuring 500m. Habitat disturbance variables were obtained from open-access databases and included distance to roads, presence and number of hurricanes, forest loss, and presence of forest fires. Ecological factors were based on data collected during vegetation surveys and included number and basal area of feeding tree species, and canopy height. We ran generalized linear mixed models and found that monkey abundance was negatively affected by forest loss but positively affected by the basal area of feeding trees. We therefore suggest that a combination of anthropogenic and ecological factors affects spider monkey abundance. Spider monkey's high degree of social flexibility may be a mechanism allowing them to adjust to changes in their environment when canopy connectivity is not lost. Our results provide policy and conservation-decision makers with key information to develop regional conservation plans. Additionally, our methods can be used to identify the factors that affect the abundance of other mammal species.

Keywords: behavioural flexibility; conservation; forest loss; population monitoring; spider monkey

INTRODUCTION

Anthropogenic and natural habitat disturbances are the major drivers of change in species abundance and distribution, currently threatening the survival of 1 million plant and animal species (Díaz et al., 2019). Forest loss increases human access to previously undisturbed areas and impacts the remnant habitat through fragmentation and edge effects (Fischer and Lindenmayer, 2007; Haddad et al., 2015). In addition, tree species producing fruits favoured by frugivores are often targeted by selective logging (Johns, 1988), or die out due to changes in microclimate (Laurance et al., 2006). The loss of these tree species may reduce the availability of food resources and lead to the decline of frugivore populations (Kirika et al., 2008) or cause animals to move into areas that are less suitable and potentially closer to human settlements (Imong et al., 2014). Given this scenario, animal species with long life histories and low population growth rates, such as many primates, may go extinct in the wild (Fahrig, 2002; van Schaik, 2013).

A large degree of variability exists in how species abundance is affected by anthropogenic disturbance, thereby justifying the need to examine individual species' responses (Irwin et al., 2010). However, results relative to these responses are often inconclusive as studies are usually limited to single sites where conditions or threats differ from other sites (Link *et al.* 2010, Kolowski and Alonso 2012), hampering their use by conservation practitioners at sites where studies have not been carried out. Recent calls have been made to examine the effects of habitat disturbance at larger spatial scales, whereby the variable of interest is compared across multiple sites (or landscapes), facilitating extrapolation of the results to other areas (Arroyo-Rodríguez and Fahrig, 2014; Ordóñez-Gómez et al., 2015).

Although habitat disturbance may jeopardize biodiversity, persistence of animal species is largely determined by a their degree of behavioural flexibility (i.e., animals' ability to change their behaviour in response to a changing environment; Komers 1997, van Schaik 2013, Beever *et al.* 2017). Aside from flexibility in maintenance activities such as foraging, social flexibility may aid animals in adapting to changing habitats. Spider monkeys (*Ateles* spp.) exhibit a high degree of social flexibility (Chapman et al., 1995; Schaffner et al., 2012), living in large groups that are rarely all together; instead, they form small subgroups that change membership over the course of the day (i.e. fission-fusion dynamics; Aureli *et al.* 2008). This social flexibility enables spider monkeys to respond rapidly to environmental changes by decreasing subgroup size when resources are limited (Rodrigues, 2017; Schaffner et al., 2012), aiding them to cope with the immediate effects of habitat disturbance, for example by foraging more efficiently (Kolowski and Alonso, 2012; Rodrigues, 2017; Schaffner et al., 2012).

Anthropogenic disturbance often occurs at an accelerated pace compared to changes in the environment caused by natural processes, affecting the survival capacity even of those species with high social flexibility. Species such as spider monkeys and chimpanzees (*Pan troglodytes*), are experiencing drastic population declines, despite their high levels of social flexibility (Ramos-Fernández and Wallace, 2008; Walsh et al., 2003). These declines may be caused by extensive habitat loss as a result of logging, high levels of hunting or outbreaks of zoonotic diseases (Strindberg et al., 2018; Walsh et al., 2003). Aspects of their life-history and dietary patterns make spider monkeys more vulnerable to the effects of anthropogenic disturbances, despite their high levels of social flexibility. Spider monkeys are highly frugivorous (Di Fiore et al., 2008), and their population abundance is positively correlated with fruit-tree abundance (Mourthé, 2014), which in turn is related to the size and quality of the habitat (Arroyo-Rodríguez and Mandujano, 2006). Previous studies demonstrate that spider monkeys in fragmented landscapes can decrease their dependence on ripe fruits by eating more leaves (Chaves et al., 2012; de Luna et al., 2017). However, higher leaf consumption may lead to decreased body condition (Wallace, 2005), and it remains unclear how the overall health and long-term survival of populations living in disturbed habitats will be affected. In addition, spider monkeys are almost completely arboreal (Campbell et al., 2005) and have large home ranges (Asensio et al., 2015), thereby requiring large areas of well-connected habitat to maintain arboreal pathways and meet their feeding requirements (Ramos-Fernández and Wallace, 2008). Their long inter-birth intervals and time to reach sexual maturity (Vick, 2008) limit the time within which declining populations can recover (Ramos-Fernández and Wallace, 2008). As a result, even though social flexibility is an effective mechanism to cope with short-term disturbance it is unclear whether it aids spider monkeys to effectively respond to accelerated, diverse, and long-term anthropogenic changes in their habitat.

We examined the effect of different types of habitat disturbance on the abundance of spider monkeys at the regional scale in the Yucatan Peninsula, Mexico. We recorded the location along the transect and the time of sighting of each independently moving spider monkey. An expanding tourism industry along Mexico's Caribbean coastline has caused rapid growth of human population and infrastructure in the Yucatan Peninsula in recent years (Ellis et al., 2017). Additionally, hurricanes and forest fires are common in the same area (Ameca et al., 2019; Bonilla-Moheno, 2012; Mascorro et al., 2016). These different sources of disturbance along with the sparse distribution of large feeding trees as a result of forest regeneration (Ramos-Fernández and Ayala-Orozco, 2003) make the Yucatan Peninsula an ideal place to study the effects of habitat disturbance on spider monkey abundance at the regional scale. We examined the effect of anthropogenic and natural disturbance, as well as ecological factors, to evaluate which are the most relevant in determining spider monkey abundance.

MATERIAL AND METHODS

Data were collected using 16 transects distributed across 4 study sites in the Yucatan Peninsula (Figure 1): Otoch Ma'ax yetel Kooh Fauna and Flora Protected Area (hereafter OMYK: 20°38' N, 87°38' W), Calakmul Biosphere Reserve (hereafter Calakmul: 18°6′ 19.41″ N, 89°48′38.98″ W), Los Arboles Tulum (hereafter Los Arboles: 20°17'50.5"N, 87°30'59.1"W), and Bala'an K'aax Fauna and Flora Protected Area (hereafter Bala'an K'aax: 19°14'58"N, 89°20’30”W). Study sites were separated by a minimum distance of 38 km. The Yucatan Peninsula is marked by a clear dry (January - May) and rainy season (June – December, see SMN, 2016).

We estimated the abundance of spider monkeys using line transect surveys (Peres 1999, Chiarello 2000, Michalski & Peres 2005). The number of transects per site depended on the size and logistical constraints of the site. When possible the distance between transects was set at a minimum of 1 km; however, the shape and size of the study area affected the orientation and distance between transects. The lengths of transects in the four study sites varied between 1.5 and 4 km (mean = 2.25 km), common transect lengths for arboreal primate surveys. The total length of sampled transects was 13 km in OMYK, 3 km in Los Arboles, 11 km in Bala’an K’aax and 9 km in Calakmul. The number of transects surveyed per site is presented in Table 1.

Each transect was walked six times throughout a full year (May 2015-June 2016; see Table 1 for the total survey effort at each site). Each transect was walked at least twice in the morning (07:00-11:00) and twice in the afternoon (14:00-18:00), at least one month apart to increase independence between replicates of the same transect and to control for the effect of seasonality on spider monkey habitat use. Transects were walked at a speed of 1.0-2.6 km/hour (mean = 1.6 km/hour), in line with the recommended speed for this species to minimize observer impact on the distribution of the study animals (Spaan et al., 2017). To ensure consistency between surveys at different sites, the same person collected the data during all transect walks. In addition, field assistants were trained in survey techniques and the identification of spider monkeys prior to starting surveys at a site to aid spider monkey detection.

DATA COLLECTION

We recorded the location along the transect and the time each independently moving spider monkey was sighted. Habitat disturbance variables were calculated from open-access databases obtained from geographical information systems and remote perception and included the distance to roads, the presence and number of hurricanes, forest loss, and the presence of forest fires.

Ecological factors were calculated from data we collected during vegetation surveys and included the number of feeding tree species, basal area of feeding trees, and canopy height (Supplementary Materials).

ECOLOGICAL FACTORS

To determine feeding tree abundance and diversity, we surveyed vegetation transects within a strip width of 2 m along the entire length of all transects used for monkey surveys. We measured all trees of a diameter at breast height (DBH) ≥ 5 cm and identified their species with the help of expert local field assistants, a botanist, and appropriate field guides (Bohn et al., 2014; Durán et al., 2000; Martínez and Galindo-Leal, 2002). Most specimen samples were verified in the herbarium at the Centro de Investigación Científica de Yucatan, Merida, Mexico. Lianas were not recorded. When trees had multiple stems, we measured each stem of DBH ≥ 5 cm separately (Worman and Chapman, 2006), and considered it as an individual tree for subsequent analyses. Canopy height was determined at 50 m intervals along the transects using a clinometer. We obtained the following ecological variables from the vegetation transects: feeding tree basal area, feeding tree species richness and canopy height. Unidentified tree species were not included in the calculations of feeding tree basal area and feeding tree species richness which may therefore have been underestimated. See Supplementary Materials for calculations of ecological and habitat disturbance variables.

DATA ANALYSIS

We divided transects into 500 m segments and calculated the spider monkey count (i.e., the number of independently moving individuals) for each segment (Rovero and Struhsaker, 2007; Serckx et al., 2016). Given that the aim of our study was to examine the effect of different types of habitat disturbance and ecological factors on the relative abundance of spider monkeys rather than calculate population density, spider monkey counts were summed for the six surveys on the same

500 m segment. A previous study on *A. geoffroyi* suggests that repeated counts of the same individual during surveys are rare (2.1% according to Spaan et al., 2017). We therefore expect any potential error introduced into monkey counts as a result of including recounted individuals to be minimal. We selected a transect segment length of 500 m to avoid a high number of segments with no sightings and few segments with many sightings (which can occur if transect segments are very short), while at the same time allowing predictor variables to be determined at a local scale (Serckx et al., 2016). We segmented transects from the start of the transect using the COGO toolbox in ArcMap 10.22.

We determined the effect of measures of anthropogenic and natural habitat disturbance and vegetation structure on spider monkey counts using a general linear mixed model (GLMM) (Barelli et al., 2015; Rovero et al., 2012). We ran a Poisson GLMM with a square root link using the glmer function of the package *lme4* (Bates et al., 2015) in the program R v. 3.2.1 (R Core Team, 2018). Spider monkey count was entered as the dependent variable into the model. The predictor variables were the distance to roads, distance to villages, forest loss, presence and number of hurricanes, the presence and number of forest fires, the number of feeding tree species, canopy height and basal area of feeding trees. Before entering predictor variables into the GLMM, all continuous variables were z-transformed to a mean of 0 and a standard deviation of 1 (Schielzeth, 2010) so that estimates could be compared irrespective of their scale (Kirkpatrick et al., 2017). We used a Variance Inflation Factor (VIF) to assess the collinearity between predictor variables (Sikkink et al., 2007). When there is collinearity between predictor variables it can be difficult to separate the independent effects of each predictor variable on the dependent variable, complicating the interpretation of the results (Rhodes et al., 2009; Freckleton et al., 2011). High VIF values (> 3) of a predictor variable indicate collinearity with the other variables (Zuur et al., 2010). The variables number of forest fires, the presence of hurricanes, and the distance to villages were excluded from further analysis due to high VIF values. We accounted for overdispersion by adding an observation-level random factor to the model (Harrison, 2014). We found no evidence of spatial autocorrelation (Moran's Index = -0.03, p = 0.89), using the Spatial Autocorrelation tool in ArcMap 10.2.2.

To control for multiple segments of the same transect, we entered transect ID as a random factor in the GLMM (Bolker et al., 2009). To control for multiple transects located at the same site, we entered Site ID as a fixed control variable in the model as there were four study sites and therefore not sufficient levels (<8 levels) to enter the variable as a random factor (Bolker, 2015). We compared the full model to a null model using a likelihood ratio test (Barelli et al., 2015; Forstmeier and Schielzeth, 2011) with the *ANOVA* function in R. The null model contained the random factor transect ID and the observation-level random factor, along with site ID as a fixed control variable. We calculated the marginal R^2 (variance explained by the predictor variables) of the full model using the r.squaredGLMM function of the package *MuMIn* (Barton, 2018; Nakagawa and Schielzeth, 2013). We do not present the conditional R^2 (variance explained by the predictor variables and random factors combined) because the value is misleading given that the observation level random effect is of little biological interest but its addition inflates the random effect variance (Harrison, 2014; Harrison et al., 2018).

RESULTS

We recorded a total of 116 individual monkeys during transect walks at the four sites for an overall encounter rate of 0.54 individuals per km walked. Sites ranged from 8 - 64 individuals and 4 -16 subgroups sighted during surveys (Table 1). Spider monkeys were sighted on 17 of the 72 transect segments (23.6%). The total number of individuals sighted in each of the 17 segments during 6 transect walks ranged from 1 to 25 and the total number of subgroups from 1 to 6.

The GLMM results confirmed that predictor variables affected individual spider monkey counts (likelihood ratio test comparing the full and null models: $X^2 = 17.23$, df = 7, p=0.016). Feeding-tree basal area was positively correlated, and forest loss negatively correlated with spider monkey counts (Table 2). Furthermore, the presence of forest fires tended to be negatively correlated with spider monkey counts (Table 2). There was no effect of distance to roads, number of hurricanes, feeding tree species richness and canopy height on spider monkey counts. The marginal R^2 value was 0.16.

DISCUSSION

Our analysis at the regional scale found that spider monkey abundance in the Yucatan Peninsula was possibly associated with anthropogenic habitat disturbance and food abundance. As expected, we found higher numbers of spider monkeys in areas with more forest and more feeding trees. Unlike previous studies on the effects of anthropogenic disturbances on spider monkeys (Link et al., 2010), our results were not obtained at single sites, but instead at 4 sites across the Yucatan Peninsula.

Forest loss is one of the main drivers of population declines of primate species (Estrada et al., 2017), including spider monkeys (Ramos-Fernández and Wallace, 2008), as they have large home range requirements and need large tracts of connected forest (Benchimol and Peres, 2013). Given that we found forest loss to affect monkey populations within protected areas, it is safe to assume that its effect outside of protected areas would be even more severe. Historically, forest loss in the Yucatan Peninsula has been associated with slash-and-burn agriculture, where cleared areas area left to regenerate after a few years of use (Dupuy et al., 2012; Hartter et al., 2008) and therefore, forest loss was often only temporal. Recently, however, forest loss has been caused by large-scale infrastructure expansion and urbanization (Ellis et al., 2017), where forest is cleared permanently and replaced with concrete structures and roads. We found no effect of the distance to roads on spider monkey counts. One possible reason is that such roads do not have a strong impact on nearby forests. For example, tree species diversity and richness in mature agroforests managed by Yucatec Mayan and Yucatec-Tzotzil villages surrounding the Calakmul Biosphere Reserve did not differ from nearby mature forests (Bohn et al., 2014). Therefore, although roads leading to villages may cause some deforestation, their floristic composition may encourage the use of these areas by spider monkeys. However, if connected forests continue to shrink or disappear in this region, we expect monkey population numbers to decline drastically. Under this scenario, it becomes imperative to protect areas of continuous forest and well-connected forest patches to ensure the sustained presence of spider monkeys in the Yucatan Peninsula.

An important source of forest loss is forest fires, which can clear away large swathes of forest and are common during the dry season in the Yucatan Peninsula (Ellis et al., 2017). We found a trend that the past occurrence of forest fires negatively affected the abundance of spider monkeys. However, the lack of collinearity between the variables forest loss and the presence of forest fires assessed through VIF indicates that forest loss affects the abundance of spider monkeys independently from forest fires.

In line with our expectations and as previous studies on primates have suggested (Hanya and Chapman, 2012), the abundance of feeding trees positively affected spider monkey abundance. Contrary to our expectation, canopy height did not affect spider monkey abundance. Canopy height is a measure of forest maturity in the Yucatan Peninsula, where forests are in differing stages of regeneration due to slash-and-burn agriculture and hurricanes (Bonilla-Moheno, 2012; Chazdon, 2014), and older forests are taller than younger forests (Dupuy et al., 2012). Our result therefore supports previous studies which have suggested the use of regenerating forest by spider monkeys (Chapman 1989, Ramos-Fernández *et al.* 2013, Arroyo-Rodríguez *et al.* 2017, Bolt *et al.* 2018), although they may prefer mature forest due to the higher availability of food (van Roosmalen and Klein, 1988). For instance, tree species important in their diet occur at much higher densities in mature compared to regenerating forest (e.g., 288 *Brosimum alicastrum* trees/ha in mature forest vs. 1 tree/ha in regenerating forest, Ramos-Fernández & Ayala-Orozco 2003). Therefore, although spider monkeys can use regenerating forest they may rely on regular access to mature forest. Mature forest fragmentation in the Yucatan Peninsula differs from other regions in Mexico where spider monkeys occur (e.g., Veracruz and Chiapas; Galán-Acedo *et al.* 2018) in that forest patches are surrounded by a matrix of forest in differing stages of regeneration (Daniels et al., 2008; Urquiza-Haas et al., 2007). This results in a patchy distribution of feeding trees and a complex network of spatially and temporally available food sources for spider monkeys. Importantly, although food availability is lower in regenerating forests (García-Licona et al., 2014), canopy connectivity is maintained, potentially allowing arboreal species with high degrees of social flexibility to use regenerating forests as a corridor connecting mature forest patches. This is because high degrees of social flexibility allow species to adjust their subgroup size and composition in relation to food availability (Schaffner et al., 2012), and may enable them to include well connected areas with low food availability into their home range. Social flexibility may therefore be a mechanism allowing spider monkeys to adapt to changes in their environment caused by natural or anthropogenic disturbances so long as canopy connectivity is not lost. To understand the importance and conservation value of regenerating forests for arboreal mammals, future studies should focus on habitat use at the regional scale and the importance of mature forest patches in a mosaic of regenerating forest, with conservation efforts focused on both maintaining mature forest and promoting forest regeneration.

By collecting data from different sites across the Yucatan Peninsula, we were able to investigate how different types of disturbance and environmental factors may affect the abundance of an endangered primate at a regional scale. Our results indicate that spider monkey abundance in the Yucatan Peninsula is driven more by overall forest loss than human infrastructure (e.g., distance to roads) and factors affecting forest structure and composition (e.g., number of hurricanes). Additionally, we suggest that it is a combination of anthropogenic and ecological factors that affect the species' abundance. Forested spider monkey habitat is being converted at an unprecedented rate along with Caribbean coastlines due to the continually expanding tourism industry and frequent forest fires in the interior areas of the Yucatan Peninsula (Ellis et al., 2017). Continued forest loss will almost certainly result in drastic spider monkey population declines. This information is extremely useful to develop regional conservation plans as the information obtained from single sites, though valuable for understanding conditions at one location, may not be applicable to other sites in the same region. We recommend similar studies be conducted on the same species at multiple locations and on other species at the same locations to draw species-specific and/or regional inferences on how habitat disturbance affects species abundance, thereby aiding conservation decision-making.

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TABLES:

Table 1: Survey effort and spider monkey encounter rates (number of individuals or subgroups per kilometer surveyed) at the four study sites.

Site	Number of transects	Number of 500m segments	Total survey effort (km)	Number of sighted individuals	Individual encounter rate	Number of sighted subgroups	Subgroup encounter rate
OMYK	4	26	78	64	0.82	16	0.21
Los Arboles	2	6	18	8	0.44	4	0.22
Bala'an K'aax	4	22	66	29	0.44	6	0.09
Calakmul	6	18	54	15	0.28	4	0.07
Total	16	72	216	116	0.54	30	0.14

Table 2: GLMM results of the effect of anthropogenic and natural habitat disturbance and ecological factors on spider monkey counts at 4 sites across the Yucatan Peninsula.

Variable	**Estimate**	**SE**	**Z**	**p**
Distance to road	0.06	0.36	0.16	0.875
Forest loss	-0.37	0.16	-2.38	0.017
Presence of forest fires	-1.00	0.54	-1.85	0.065
Number of hurricanes	-0.14	0.28	-0.49	0.622
Feeding tree species richness	-0.38	0.26	-1.45	0.148
Basal area of feeding trees	0.39	0.14	2.82	0.005
Canopy height	0.14	0.14	0.94	0.35

FIGURES:

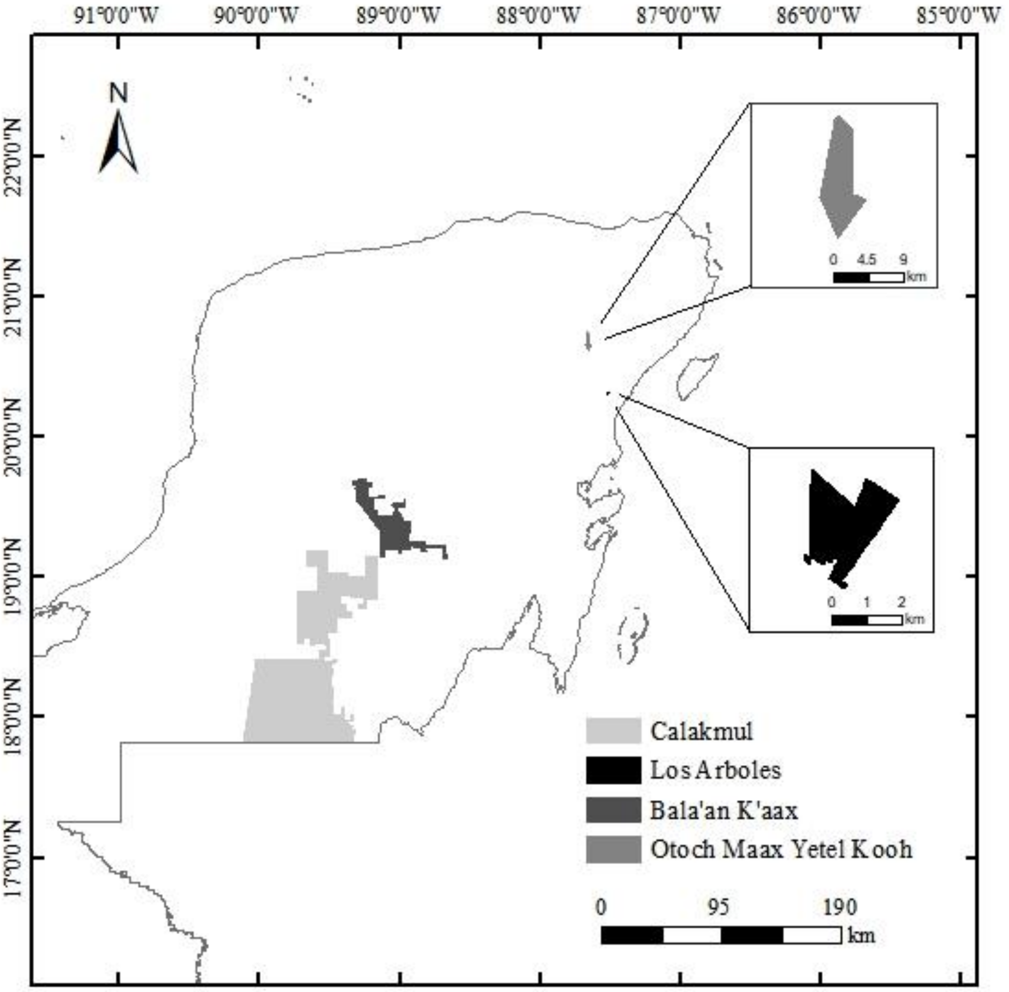

Figure 1: Map of four study sites to assess the role of habitat disturbance and habitat characteristics on Geoffroy's spider monkey abundance in the Yucatan Peninsula, Mexico. A total of 16 transects (36,000m of line transects), were distributed across study sites.