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How survey design affects monkey counts: A case study on individually recognized spider monkeys (Ateles geoffroyi)

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Abstract

The fast movement and high degree of fission-fusion dynamics of spider monkeys (Ateles spp.) make them notoriously difficult to survey. We examined which aspects of survey design affect spider monkey sightings along transects on a group of individually recognized spider monkeys (A. geoffroyi) in Punta Laguna, Yucatan, Mexico. We calculated the number of monkeys and subgroups sighted per transect walk. Using generalized linear models, we found no effect of the number of observers, transect type (new vs. existing), walking speed, or time of day on individual monkey counts and subgroup counts. Recounting individuals was relatively rare and occurred when transects were walked relatively slowly. We missed more young than adult monkeys. The group composition based on survey data was similar to the known group composition. Based on our findings we recommend that surveys performed on relatively flat terrain be conducted at speeds similar or faster than the moving speed of spider monkeys to minimize recounting individuals and that young : adult female ratios based on survey data be interpreted as conservative indicators of population health. The novel methods presented to determine sources of bias in population estimates are applicable to a wide range of primates that are difficult to survey.

Keywords: population monitoring, fission-fusion dynamics, missing individuals, Ateles geoffroyi

Introduction

Line transect surveys are the most commonly used method to survey arboreal primates (Peres, 1999; Buckland et al., 2010a, 2010b), providing abundance (hereafter population density, e.g. individuals per km^2) or relative abundance estimates (hereafter encounter rate, e.g. individuals per km), which form the base of a wide variety of studies in ecology and conservation and aid in the formulation of species management plans. The number of monkeys sighted may be affected by survey design, which in turn may affect population density estimates or encounter rates.

Survey design is often limited by field conditions, but only a handful of studies have investigated how survey design affects primate population estimates. Firstly, primate surveys are commonly performed in the morning and late afternoon (Peres, 1999; Ingberman et al., 2009) as primates are more likely to be encountered during periods of heightened activity (Chapman et al., 1988; Peres, 1999), yet there is no general trend on how time of day affects encounter rate or population density (Ingberman et al., 2009; Kun-Rodrigues et al., 2013; Lee et al., 2014; Matsuda et al., 2016). For instance, early morning is the optimum time to survey gibbons (Hylobates agilis; Lee et al., 2014), whereas time of day did not affect either howler monkey (Alouatta clamitans) or sifakas (Propithecus coquereli) population estimates (Ingberman et al., 2009; Kun-Rodrigues et al., 2013). Secondly, the effects of survey speed on encounter rate remain poorly investigated (Shupe et al., 1987; Iwanaga & Ferrari, 2002; Aliaga-Rossel et al., 2006; Nekaris et al., 2014), despite its importance to detectability. Thirdly, line transect surveys are typically performed by a group of one to two observers. Studies examining the effect of the number of observers on encounter rate or population density estimates are limited and suggest that the number of observers does not affect primate encounter rate (Nijman & Menken, 2005; Haus et al., 2009).

Understanding how study design affects encounter rates may be especially important for species that are difficult to survey (often providing low encounter rates) such as those with high degrees of fission-fusion dynamics (i.e., a high temporal variation in the degree of spatial cohesion and individual membership in subgroups: Aureli et al., 2008) and fast arboreal movement, such as spider monkeys (Ateles spp.: Symington, 1990; Chapman et al., 1995). These characteristics make it problematic to meet at least two of the assumptions of line transect surveys (Buckland et al., 2001, 2010a, 2010b; Ross & Reeve, 2011): 1) groups or individuals are detected before they respond to the observer by fleeing, and the non-responsive speed (i.e. a movement which is independent of the observer's presence) of the animal is slower than the observers speed; and 2) group sizes are recorded precisely and groups are not counted twice.

Violating the assumptions of line transect surveys could lead to inaccurate population estimates. Fast movement enables spider monkeys to flee out of the observer's sight before they are detected. Walking at a speed that is faster than the commonly used 1 km/hour may counter the problem of non-responsive movement (Plumptre et al., 2013), as the observers' speed is closer to the study species' speed. Although it has been suggested that subgroup size can be measured instead of group size for species with high degrees of fission-fusion dynamics (Peres, 1999), subgroup size changes in relation to fruit availability (Chapman et al., 1995; Pinacho-Guendulain & Ramos-Fernández, 2017) and the average subgroup size differs between seasons (Hashimoto et al. 2003; Asensio et al. 2009) whereas group size remains the same. It is difficult to ensure that the same group, subgroup or individuals are not counted multiple times. Despite this potentially common violation, to date no primate studies have aimed to investigate how often the same individual or group is detected at various points on the same transect during the same transect walk.

Our study aimed to examine which aspects of survey design affect spider monkey sightings along transects and determine whether two relevant assumptions of line transect sampling are violated. To do so, we surveyed a group of individually recognized spider monkeys. We use the findings to provide recommendations for the design of surveys for animals exhibiting fast movement and high degrees of fission-fusion dynamics.

Method

Study site and subjects

We collected data between October 2014 and January 2015 in the Otoch Ma'ax yetel Kooh Flora and Fauna Protected Area (20°38' N, 87°38' W, 14 m above sea level, Figure 1) near the village of Punta Laguna, Yucatan, Mexico. Geoffroy's spider monkeys (Ateles geoffroyi) have been continuously studied in the protected area over the past 20 years (Ramos-Fernández et al., in press). The study group included 36 individually identifiable monkeys older than one year: four adult males, one subadult male, 12 adult females, five subadult females and 14 young. We defined young as individuals younger than five years but older than one year, given that infants less than one year still cling to their mother's bodies for large periods of time and individuals younger than five years are found in the same subgroup as their mother (Vick, 2008). Subadults were individuals between five and eight years old, being sexually mature, but not fully-grown, and adults were individuals older than eight years (Shimooka et al., 2008). Females can be easily distinguished from adult males based on the presence of a protruding clitoris. The group included 11 mother-young dyads based on continuously updated demographic records.

We used an existing transect and a newly cut transect of the same length (919 m; Table 1). To increase the likelihood of monkey sightings we selected the existing transect from the trail system as spider monkeys used the area around the selected trail during the same period the previous year. We opened the newly cut transect roughly parallel to the existing transect (Figure 1). Both transects were located on a relatively flat terrain with only a few large boulders.

Survey design

We performed surveys according to the line transect method (Peres, 1999). We walked transects at a speed of 1.0-2.0 km per hour visually scanning all levels of vegetation and listening for spider monkeys. We performed surveys twice daily for most survey days, without walking the same transect more than three times per day. We did not consider multiple walks per day on the same transect to be problematic because two walks of the same transect are considered independent if separated by a few hours (Peres, 1999); this would not be appropriate for slower moving primates. Additionally, the spider monkeys in our study group have large daily traveling distances (1.18 km – 3.87 km; Ramos-Fernández and Ayala-Orozco, 2003). The first author was an observer in all surveys. Transect walks were performed by one, two or three observers and in one of three time blocks covering all hours of the day in which spider monkeys were active (Table 1).

Data collection

During each survey we collected the following data: start and end time, date of survey, number of observers, and we noted whether the transect was newly cut or existing. When monkeys were sighted during line transect surveys, we spent no more than ten minutes collecting data on subgroup size, composition, time of sighting and location (using a handheld GPS device).

We collected data on subgroup composition by categorizing independently-moving monkeys into two age classes: adult and young. Adults were distinguished from young based on the size of the individual and facial coloration (Vick, 2008). We included subadult individuals in the adult class as they are difficult to distinguish from adults during surveys. We excluded infants clinging to their mothers from the analyses as they may often be obscured from view.

During 2- and 3-observer transect walks, spider monkeys were individually recognized by trained field assistants (with 20 years of experience in identifying spider monkeys) and the identity of all sighted monkeys was recorded. We assigned each sighted individual to its age-class based on its identity. This was possible since subgroups included on average (mean ±SE) 2.7 ± 0.17 independently moving individuals; this would not be possible for species that move in larger groups.

Data analyses

Aspects of study design

We ran generalized linear models (GLMs) to determine the effect of the number of observers (one, two or three), walking speed (continuous from 1.0 to 2.0 km/hour), and time of the day in which the survey was carried out (06:00-10:00, 10:01-14:00 or 14:01-

18:00) on individual counts (i.e., number of sighted monkeys) or subgroup counts (i.e., number of sighted subgroups). We ran two sets of models with walking speed calculated in different ways. We calculated walking speed including the time to record monkey sightings for one set of models and excluding such recording time for the other set of models. We used variance inflation factor (VIF) to assess the collinearity between predictor variables. All VIF values were below two indicating that there was no collinearity between predictor variables (Rhodes et al., 2009). Typically, Poisson distributions are used to model count data (Richards, 2015). After checking for overdispersion (Buckley, 2015), we modeled individual counts and subgroup counts using negative binomial distributions. We created negative binomial GLMs using the glm.nb function of the package MASS (Ripley et al., 2013) in the program R v. 3.2.1 (R Core Team, 2016). We entered month and transect type (newly cut vs. existing trail) as control variables in all models to account for the potential effect of a different distribution of food sources across months and repeat transect walks on the same transects. We compared the full models to null models including only the control variables (month and transect type) using a likelihood ratio test (Forstmeier & Schielzeth, 2011), with the ANOVA function in R. Statistical significance was set at $P<0.05$.

Assumptions for line transect surveys

During 2- and 3-observer transect walks we used the individual identity of the spider monkeys to determine whether individuals were sighted multiple times during the same transect walk (recounted individuals). We calculated the percentage of individuals that were recounted by dividing the total number of recounted individuals by the total number of individuals that were encountered and multiplying this figure by 100. To determine whether walking speed affects recounting individuals, we divided transect walks into slowly walked when walking speed was 1.0-1.49 km/h (n=70) and rapidly walked when speed was 1.5-2.0 km/h (n=32). We selected these two speed categories as previous line transect surveys of spider monkeys have been walked at speeds below or above 1.5 km/h (>1.5 km/hour: Cant, 1978; Iwanaga & Ferrari, 2002b; Ravetta & Ferrari, 2009; <1.5 km/hour: Weghorst, 2007; Link et al., 2010; Aquino et al., 2012; Kolowski & Alonso, 2012; Méndez-Carvajal, 2013).

Given that we knew the demographic composition of the group, in 2- and 3-observer transect walks we could establish when we missed the mother of a sighted young or we missed the young of a sighted mother. We calculated the proportion of missed individuals per transect and age class by dividing the total number of missed individuals by the total number of individuals that should have been present in the encountered subgroups (i.e. all sighted and missed individuals) during all walks of one transect. This analysis was limited to mother-infant dyads as we could not determine whether other individuals were missed during surveys. To determine whether more individuals were missed if they were at greater distances from the transect centerline, we considered the perpendicular distance from each missed individual as the mean of the perpendicular distances from all sighted members of the same subgroup. We then compared these mean values to the distribution of the corresponding mean values for all sighted subgroups.

Using survey data without taking into account individual identities, we calculated the proportion of adult males, adult females and young by dividing the number of individuals of each age-sex class by the total number of sighted individuals (i.e., adult males, adult females and young). We compared proportions obtained from the survey data to the proportions based on the known group composition.

We calculated the young : adult female ratio of individuals distinguishing adult females from young simply based on size and facial markings. We performed this calculation using only individuals observed during 2- and 3-observer walks as we also calculated the ratio excluding subadult females based on their identity. We compared this ratio to the ratio based on the actual group composition and to ratios including missed young and/or missed adult females.

Results

In the 102 transect walks (Table 1), for a total survey effort of 93.74 km, we sighted 280 spider monkeys (newly cut transect: 126; existing transect: 154) in 103 subgroups (newly cut transect: 48; existing transect: 55). The mean (±SE) size of encountered subgroups was 2.7 ± 0.17 (newly cut transect: 2.7 ± 0.28, range: 1-12; existing transect: 2.8 ± 0.21, range: 1-6). The size distribution for encountered subgroups during surveys was similar to that for subgroups found by other researchers in the same area during the study period (77% of encountered subgroups fell within the first and third quartiles of the size distribution of subgroups found by other researchers). The number of sighted spider monkeys during each time block and in relation to the number of observers is presented in Table 1.

Full-null model comparisons found that the predictor variables did not affect individual spider monkey counts including (χ^2=7.06, df=5, p=0.22) or excluding the time to record individuals (χ^2=7.04, df=5, p=0.22). Similarly, the predictor variables did not affect spider monkey subgroup counts including (χ^2=10.69, df=5, p=0.06) or excluding recording time (χ^2=10.62, df= 5, p=0.06).

During 2- and 3-observer transect walks we sighted a total of 237 spider monkeys older than one year in 89 subgroups including 115 adult females and 93 young. Recounting individuals was relatively rare, with only five monkeys reencountered during the same transect walks (three on the newly cut transect and two on the existing transect), which is 2.1% of the encountered monkeys in 3.3% of the encountered subgroups (three of the 89 subgroups) (Table 2). No monkey was recounted more than once. Subgroup composition changed between the first and second sighting (Table 2). The five instances of recounting individuals occurred on three separate transect walks (Table 2). All five cases of recounting occurred when transects were walked slowly (i.e. 1.0-1.49 km/h).

There was no clear effect of walking speed on missing individuals. When we walked transects slowly seven individuals were missed (two adult females and five young), whereas nine individuals (all young) were missed when we walked transects walked fast. A larger number of young were missed than adult females during surveys, two adult females (one on each transect) were missed, representing 1.7% of the encountered adult female monkeys (115 sighted and two missed); 14 young (seven on each transect) were missed, representing 13.1% of the encountered young (93 sighted and 14 missed). The number of individuals missed during surveys did not appear to increase with increasing perpendicular distance from the transect (80% of perpendicular distance means for subgroups with missed individuals fell within the first and third quartiles of the distribution of all subgroup perpendicular distance means).

Using survey data without taking into account individual identities, the proportions of adult males, adult females and young were 0.10, 0.48, 0.42, respectively; whereas the corresponding proportions based on the known group composition were 0.14, 0.47 and 0.39. The young : adult female ratio for the survey data was 0.81. When both missed adult females and young were included, the ratio equaled 0.91. The young : adult female ratio based on the actual group composition (14 young and 12 adult females) was 1.17, but when the 5 subadult females were combined with the 12 adult females the ratio was 0.82.

Discussion

We found no effect of time of day, walking speed and number of observers on individual spider monkey and subgroup counts. Although spider monkey activity peaks in the early morning and late afternoon (Green, 1978; Wallace, 2001), corresponding to peaks in encounter rate (Green, 1978), we found no effect of time of day on spider monkey counts. Similar to our results, spider monkey (A. hybridus) surveys done in forest fragments found no effect of time of day on encounter rate (Marsh et al., 2016). Previous studies on Atelines (Ateles chamek and Lagothrix cana) support our findings as walking speed did not affect encounter rate (Iwanaga & Ferrari, 2002).

The spider monkeys inhabiting Otoch Ma'ax yetel Kooh are highly habituated to human presence as ecotourism has been the major source of income in the Punta Laguna village for more than 14 years, and guides enter the forest with small groups of tourists at least once per day. It is therefore likely that the number of observers would not affect spider monkeys' behavior and therefore their sighting along transects at the study site. Surveys of arboreal and terrestrial unhabituated primates, including fast moving gibbons (Hylobates muelleri), found no effect of the number of observers on counts (Nijman & Menken, 2005; Haus et al., 2009), suggesting that our results may be applicable to unhabituated groups of spider monkeys, and other primates with fast arboreal movement or high degrees of fission fusion dynamics.

Otoch Ma’ax yetel Kooh is a highly seasonal environment with marked dry and wet seasons. The study was carried out during the wet season when canopy cover is at its fullest and detectability is most difficult, a situation as similar as possible to other tropical rainforest environments. It must be noted that the canopy height in the study area is up to around 25 m, lower than other spider monkey habitats (Medellín and Equihua, 1998). Although low canopy may enhance detectability, the average height at which spider monkeys (A. belzebuth belzebuth) feed in taller forests (16.6 m; Dew, 2005) is around the same height as the canopy at our study site. Our results should therefore be applicable to spider monkeys living in less seasonal habitats with taller canopies.

The low number of recounted individuals suggests that the fast movement of spider monkeys (mean ± SE: 1.6 ± 0.4 km/hour at the study site; Ramos-Fernández, unpublished data) does not affect recounting when the observers walk at a comparable speed. The high degree of fission-fusion dynamics may explain why recounted spider monkeys were found in different subgroups between first and second encounters. During surveys of species that form cohesive groups, surveyors may avoid recounting by excluding groups that have the same size and composition as previously encountered. Our results show that for species with high degrees of fission-fusion dynamics this approach does not work as subgroup size and composition can change quickly and over short distances (Table 1). This potential problem is likely minimal as we only recounted 2.1% of the encountered monkeys. All five cases of recounting occurred when we walked transects at a speed of <1.5 km/hour, suggesting that walking slowly may increase the chance of recounting spider monkeys, but this interpretation awaits confirmation given our small sample sizes. To our knowledge this is the first study examining the recounting of individuals and subgroups. The difficulty to ensure that the same group, subgroup or individuals are not counted multiple times does not apply only to spider monkeys. It would be beneficial if similar studies were performed on other individually identified populations of primates with similar or lower levels of fission-fusion dynamics and movement to understand the potential effect on population surveys. Understanding how quickly the same individuals or subgroups are recounted during surveys can greatly improve survey designs. Repeating transect walks sooner than the time needed to insure independence would result in repeated counts of the same individuals and groups. Our results demonstrate that for spider monkeys the same transect can be walked repeatedly within short time periods. The time required to insure independence of transect walks differs between primate species. The time between walking the same transect is critical for slow moving species, which may remain on the same transect for days or weeks. For instance, Alouatta palliata move on average 381 m per day (Garber and Jelinek, 2006).

More young went undetected during surveys than adult females. The proportion of adult females that went undetected during surveys was low (1.7%). Given that male spider monkeys tend to move faster than females (Shimooka, 2005), we cannot assume that a similar proportion of males may have been missed, despite the lack of sexual dimorphism in spider monkeys (Rosenberger et al., 2008). Based on this consideration and the actual number of adult females and young that were missed, it is possible that more than 10% of individuals over the age of one year went undetected during surveys, thereby potentially violating the assumption that groups are counted accurately. It is therefore vital to report sources of error and confidence intervals of population density estimates and encounter rates.

Surveyors often collect data on group composition, but little evidence exists as to whether these proportions reflect the actual group composition. The proportion of adult females and young were similar between the survey data without using individual identities (0.48 and 0.42) and the actual group composition (0.47 and 0.39), suggesting that surveys are reliable sources of information of group composition for these age-sex classes. These proportions fell within those of adult females and young reported for other spider monkey populations (adult females: 0.33 – 0.52, young: 0.20 – 0.45; Shimooka et al., 2008). The proportion of adult males was only slightly lower using the survey data (0.10) than the actual group composition (0.14). Both proportions are on the lower end of those recorded for spider monkey populations (0.14 - 0.36) and lower than other populations of Ateles geoffroyi (0.2 - 0.26). These results confirm that group composition data collected during surveys are reliable. This is particularly important for studies that compare group composition in different areas, for instance, areas undergoing different anthropogenic threats.

Surveys are often performed in unexplored areas and may aim to provide information on population health using the young : adult female ratio (Fedigan & Jack, 2001). All the ratios we calculated to evaluate the issues of missing individuals and misclassifying subadult females during surveys fell within the young : adult female ratios of other spider monkey populations (0.36 - 1.31; Shimooka et al., 2008). The young : adult female ratio obtained from the survey data, in which we did not distinguish subadult females from adult females, was 0.81. When we added the number of subadult females to the actual number of adult females in the group the ratio was 0.82, showing a high accuracy of estimates based on survey data. Missing young disproportionally relative to adult females during surveys (13.1% vs 1.7%) can negatively bias the young : adult ratio. The ratio obtained from our survey data (0.81) was lower than the ratio when missed individuals were included (0.91). Based on the underestimated young : adult female ratio the population would appear less healthy than it actually is, although this is arguably preferable to overestimating the ratio, in terms of the consequences for conservation. Distinguishing nulliparous subadult females from adult females during population surveys may be problematic due to their similar size and thus several studies did not distinguish between subadult and adult females (Struhsaker, 1981; Fedigan & Jack, 2001; Treves, 2001). As subadult females had yet to contribute reproductively to the population, their inclusion in the adult female age class negatively biases the young : adult female ratio. In our study, the young : adult female ratio obtained from the survey data (0.81), in which subadult females were likely included as adult females, is lower than the ratio based on only the actual number of adult females in the group during the study period (1.17), which would again suggest that the population is less healthy than it actually is. We therefore advise that ratios based on survey data be interpreted as conservative indicators of population health. For species in which subadult females can be clearly distinguished from adult females during surveys, biases may be reduced.

There is an increasing need to standardize survey techniques so that population estimates of the same species can be compared across its range. Our results show that aspects of survey design do not affect spider monkey counts, suggesting that surveys can be successfully adapted to the logistical constraints of the survey site. Additionally, our study provided the first evidence that recounting of individuals during the same transect walk was relatively rare and that young were missed more often than adult females. We recommend that similar studies be performed on individually identifiable primate populations to understand potential sources of bias in population estimates and young : adult female ratios. Based on our findings we recommend that surveys performed in relatively flat terrain be conducted at a speed similar or faster than the moving speed of spider monkeys to minimize recounting individuals. Our research contributes to improving and standardizing line transect survey methods for spider monkeys and other species with fast arboreal movement and/**or** a high degree of fission-fusion dynamics. Many primates living in dense tropical forests are difficult to survey because they live in large, widely dispersed groups (e.g. red colobus, long-tailed macaques, uakaris), in which multiple individuals may be obscured from view or may flee before detection due to their fast movement. The novel methods presented in this article evaluating recounting, missing individuals, subgroup composition, and young : adult female ratios are applicable to a wide range of primate species that are difficult to survey and for which it is particularly important to determine potential sources of bias.

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Tables and Figures

Table 1: The number of walks performed on each transect in relation to the number of observers and time block. The number of sighted monkeys is presented in brackets.

Table 2: Age-sex classes of recounted individual spider monkeys during the same transect walk.

Figure 1: Location of the two line transects for the study site in the Otoch Ma’ax yetel Kooh (OMYK) Flora and Fauna Protected Area.