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1 **How survey design affects monkey counts: A case study on**
2 **individually recognized spider monkeys (*Ateles geoffroyi*)**
3

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36 **Abstract**

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

53

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

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58 Introduction

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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 km²) 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.

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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

82 number of observers does not affect primate encounter rate (Nijman & Menken, 2005; Haus
83 et al., 2009).

84 Understanding how study design affects encounter rates may be especially
85 important for species that are difficult to survey (often providing low encounter rates) such
86 as those with high degrees of fission-fusion dynamics (i.e., a high temporal variation in the
87 degree of spatial cohesion and individual membership in subgroups: Aureli et al., 2008) and
88 fast arboreal movement, such as spider monkeys (*Ateles* spp.: Symington, 1990; Chapman
89 et al., 1995). These characteristics make it problematic to meet at least two of the
90 assumptions of line transect surveys (Buckland et al., 2001, 2010a, 2010b; Ross & Reeve,
91 2011): 1) groups or individuals are detected before they respond to the observer by fleeing,
92 and the non-responsive speed (i.e. a movement which is independent of the observer's
93 presence) of the animal is slower than the observers speed; and 2) group sizes are recorded
94 precisely and groups are not counted twice.

95 Violating the assumptions of line transect surveys could lead to inaccurate
96 population estimates. Fast movement enables spider monkeys to flee out of the observer's
97 sight before they are detected. Walking at a speed that is faster than the commonly used 1
98 km/hour may counter the problem of non-responsive movement (Plumptre et al., 2013), as
99 the observers' speed is closer to the study species' speed. Although it has been suggested
100 that subgroup size can be measured instead of group size for species with high degrees of
101 fission-fusion dynamics (Peres, 1999), subgroup size changes in relation to fruit availability
102 (Chapman et al., 1995; Pinacho-Guendulain & Ramos-Fernández, 2017) and the average
103 subgroup size differs between seasons (Hashimoto et al. 2003; Asensio et al. 2009) whereas
104 group size remains the same. It is difficult to ensure that the same group, subgroup or
105 individuals are not counted multiple times. Despite this potentially common violation, to

106 date no primate studies have aimed to investigate how often the same individual or group is
107 detected at various points on the same transect during the same transect walk.

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

113 **Method**

114 **Study site and subjects**

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

127 distinguished from adult males based on the presence of a protruding clitoris. The group
128 included 11 mother-young dyads based on continuously updated demographic records.

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

135 **Survey design**

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

147

148 **Data collection**

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

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

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

166

167 **Data analyses**

168 *Aspects of study design*

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

172 18:00) on individual counts (i.e., number of sighted monkeys) or subgroup counts (i.e.,
173 number of sighted subgroups). We ran two sets of models with walking speed calculated in
174 different ways. We calculated walking speed including the time to record monkey sightings
175 for one set of models and excluding such recording time for the other set of models. We
176 used variance inflation factor (VIF) to assess the collinearity between predictor variables.
177 All VIF values were below two indicating that there was no collinearity between predictor
178 variables (Rhodes et al., 2009). Typically, Poisson distributions are used to model count
179 data (Richards, 2015). After checking for overdispersion (Buckley, 2015), we modeled
180 individual counts and subgroup counts using negative binomial distributions. We created
181 negative binomial GLMs using the `glm.nb` function of the package MASS (Ripley et al.,
182 2013) in the program R v. 3.2.1 (R Core Team, 2016). We entered month and transect type
183 (newly cut vs. existing trail) as control variables in all models to account for the potential
184 effect of a different distribution of food sources across months and repeat transect walks on
185 the same transects. We compared the full models to null models including only the control
186 variables (month and transect type) using a likelihood ratio test (Forstmeier & Schielzeth,
187 2011), with the ANOVA function in R. Statistical significance was set at $P < 0.05$.

188

189 *Assumptions for line transect surveys*

190 During 2- and 3-observer transect walks we used the individual identity of the
191 spider monkeys to determine whether individuals were sighted multiple times during the
192 same transect walk (recounted individuals). We calculated the percentage of individuals
193 that were recounted by dividing the total number of recounted individuals by the total
194 number of individuals that were encountered and multiplying this figure by 100. To
195 determine whether walking speed affects recounting individuals, we divided transect walks

196 into slowly walked when walking speed was 1.0-1.49 km/h (n=70) and rapidly walked
197 when speed was 1.5-2.0 km/h (n=32). We selected these two speed categories as previous
198 line transect surveys of spider monkeys have been walked at speeds below or above 1.5
199 km/h (>1.5 km/hour: Cant, 1978; Iwanaga & Ferrari, 2002b; Ravetta & Ferrari, 2009; <1.5
200 km/hour: Weghorst, 2007; Link et al., 2010; Aquino et al., 2012; Kolowski & Alonso,
201 2012; Méndez-Carvajal, 2013).

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

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

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

225 **Results**

226 In the 102 transect walks (Table 1), for a total survey effort of 93.74 km, we sighted
227 280 spider monkeys (newly cut transect: 126; existing transect: 154) in 103 subgroups
228 (newly cut transect: 48; existing transect: 55). The mean (\pm SE) size of encountered
229 subgroups was 2.7 ± 0.17 (newly cut transect: 2.7 ± 0.28 , range: 1-12; existing transect: 2.8
230 ± 0.21 , range: 1-6). The size distribution for encountered subgroups during surveys was
231 similar to that for subgroups found by other researchers in the same area during the study
232 period (77% of encountered subgroups fell within the first and third quartiles of the size
233 distribution of subgroups found by other researchers). The number of sighted spider
234 monkeys during each time block and in relation to the number of observers is presented in
235 Table 1.

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

241 During 2- and 3-observer transect walks we sighted a total of 237 spider monkeys
242 older than one year in 89 subgroups including 115 adult females and 93 young. Recounting
243 individuals was relatively rare, with only five monkeys reencountered during the same
244 transect walks (three on the newly cut transect and two on the existing transect), which is
245 2.1% of the encountered monkeys in 3.3% of the encountered subgroups (three of the 89
246 subgroups) (Table 2). No monkey was recounted more than once. Subgroup composition
247 changed between the first and second sighting (Table 2). The five instances of recounting
248 individuals occurred on three separate transect walks (Table 2). All five cases of recounting
249 occurred when transects were walked slowly (i.e. 1.0-1.49 km/h).

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

261 Using survey data without taking into account individual identities, the proportions
262 of adult males, adult females and young were 0.10, 0.48, 0.42, respectively; whereas the
263 corresponding proportions based on the known group composition were 0.14, 0.47 and
264 0.39. The young : adult female ratio for the survey data was 0.81. When both missed adult

265 females and young were included, the ratio equaled 0.91. The young : adult female ratio
266 based on the actual group composition (14 young and 12 adult females) was 1.17, but when
267 the 5 subadult females were combined with the 12 adult females the ratio was 0.82.

268

269 **Discussion**

270

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

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

287 spider monkeys, and other primates with fast arboreal movement or high degrees of fission
288 fusion dynamics.

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

298 The low number of recounted individuals suggests that the fast movement of spider
299 monkeys (mean \pm SE: 1.6 ± 0.4 km/hour at the study site; Ramos-Fernández, unpublished
300 data) does not affect recounting when the observers walk at a comparable speed. The high
301 degree of fission-fusion dynamics may explain why recounted spider monkeys were found
302 in different subgroups between first and second encounters. During surveys of species that
303 form cohesive groups, surveyors may avoid recounting by excluding groups that have the
304 same size and composition as previously encountered. Our results show that for species
305 with high degrees of fission-fusion dynamics this approach does not work as subgroup size
306 and composition can change quickly and over short distances (Table 1). This potential
307 problem is likely minimal as we only recounted 2.1% of the encountered monkeys. All five
308 cases of recounting occurred when we walked transects at a speed of <1.5 km/hour,
309 suggesting that walking slowly may increase the chance of recounting spider monkeys, but

310 this interpretation awaits confirmation given our small sample sizes. To our knowledge this
311 is the first study examining the recounting of individuals and subgroups. The difficulty to
312 ensure that the same group, subgroup or individuals are not counted multiple times does not
313 apply only to spider monkeys. It would be beneficial if similar studies were performed on
314 other individually identified populations of primates with similar or lower levels of fission-
315 fusion dynamics and movement to understand the potential effect on population surveys.
316 Understanding how quickly the same individuals or subgroups are recounted during
317 surveys can greatly improve survey designs. Repeating transect walks sooner than the time
318 needed to insure independence would result in repeated counts of the same individuals and
319 groups. Our results demonstrate that for spider monkeys the same transect can be walked
320 repeatedly within short time periods. The time required to insure independence of transect
321 walks differs between primate species. The time between walking the same transect is
322 critical for slow moving species, which may remain on the same transect for days or weeks.
323 For instance, *Alouatta palliata* move on average 381 m per day (Garber and Jelinek, 2006).

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

332 sources of error and confidence intervals of population density estimates and encounter
333 rates.

334 Surveyors often collect data on group composition, but little evidence exists as to
335 whether these proportions reflect the actual group composition. The proportion of adult
336 females and young were similar between the survey data without using individual identities
337 (0.48 and 0.42) and the actual group composition (0.47 and 0.39), suggesting that surveys
338 are reliable sources of information of group composition for these age-sex classes. These
339 proportions fell within those of adult females and young reported for other spider monkey
340 populations (adult females: 0.33 – 0.52, young: 0.20 – 0.45; Shimooka et al., 2008). The
341 proportion of adult males was only slightly lower using the survey data (0.10) than the
342 actual group composition (0.14). Both proportions are on the lower end of those recorded
343 for spider monkey populations (0.14 - 0.36) and lower than other populations of *Ateles*
344 *geoffroyi* (0.2 - 0.26). These results confirm that group composition data collected during
345 surveys are reliable. This is particularly important for studies that compare group
346 composition in different areas, for instance, areas undergoing different anthropogenic
347 threats.

348 Surveys are often performed in unexplored areas and may aim to provide
349 information on population health using the young : adult female ratio (Fedigan & Jack,
350 2001). All the ratios we calculated to evaluate the issues of missing individuals and
351 misclassifying subadult females during surveys fell within the young : adult female ratios
352 of other spider monkey populations (0.36 - 1.31; Shimooka et al., 2008). The young : adult
353 female ratio obtained from the survey data, in which we did not distinguish subadult
354 females from adult females, was 0.81. When we added the number of subadult females to

355 the actual number of adult females in the group the ratio was 0.82, showing a high accuracy
356 of estimates based on survey data. Missing young disproportionately relative to adult
357 females during surveys (13.1% vs 1.7%) can negatively bias the young : adult ratio. The
358 ratio obtained from our survey data (0.81) was lower than the ratio when missed individuals
359 were included (0.91). Based on the underestimated young : adult female ratio the
360 population would appear less healthy than it actually is, although this is arguably preferable
361 to overestimating the ratio, in terms of the consequences for conservation. Distinguishing
362 nulliparous subadult females from adult females during population surveys may be
363 problematic due to their similar size and thus several studies did not distinguish between
364 subadult and adult females (Struhsaker, 1981; Fedigan & Jack, 2001; Treves, 2001). As
365 subadult females had yet to contribute reproductively to the population, their inclusion in
366 the adult female age class negatively biases the young : adult female ratio. In our study, the
367 young : adult female ratio obtained from the survey data (0.81), in which subadult females
368 were likely included as adult females, is lower than the ratio based on only the actual
369 number of adult females in the group during the study period (1.17), which would again
370 suggest that the population is less healthy than it actually is. We therefore advise that ratios
371 based on survey data be interpreted as conservative indicators of population health. For
372 species in which subadult females can be clearly distinguished from adult females during
373 surveys, biases may be reduced.

374 There is an increasing need to standardize survey techniques so that population
375 estimates of the same species can be compared across its range. Our results show that
376 aspects of survey design do not affect spider monkey counts, suggesting that surveys can be
377 successfully adapted to the logistical constraints of the survey site. Additionally, our study

378 provided the first evidence that recounting of individuals during the same transect walk was
379 relatively rare and that young were missed more often than adult females. We recommend
380 that similar studies be performed on individually identifiable primate populations to
381 understand potential sources of bias in population estimates and young : adult female ratios.
382 Based on our findings we recommend that surveys performed in relatively flat terrain be
383 conducted at a speed similar or faster than the moving speed of spider monkeys to
384 minimize recounting individuals. Our research contributes to improving and standardizing
385 line transect survey methods for spider monkeys and other species with fast arboreal
386 movement and/or a high degree of fission-fusion dynamics. Many primates living in dense
387 tropical forests are difficult to survey because they live in large, widely dispersed groups
388 (e.g. red colobus, long-tailed macaques, uakaris), in which multiple individuals may be
389 obscured from view or may flee before detection due to their fast movement. The novel
390 methods presented in this article evaluating recounting, missing individuals, subgroup
391 composition, and young : adult female ratios are applicable to a wide range of primate
392 species that are difficult to survey and for which it is particularly important to determine
393 potential sources of bias.

394

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407

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569 **Tables and Figures**

570

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

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

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