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

D. Spaan[1,2], G. Ramos-Fernández[2,3,4], C.M. Schaffner[1,2], B. Pinacho-Guendulain[3,5] and F. Aureli[1,2,6]

1. Instituto de Neuroetología, Universidad Veracruzana, Avenida Dr. Luis Castelazo s/n Colonia Industrial Animas C.P. 91000, Xalapa, Veracruz, Mexico.
2. ConMonoMaya A.C., Chemax, Yucatan, Mexico.
3. Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca, Instituto Politécnico Nacional, Oaxaca, Mexico.
4. Centro de Ciencias de la Complejidad, Universidad Nacional Autónoma de Mexico, Mexico City, Mexico.
5. Conservación de la Biodiversidad del Usumacinta A. C., Emiliano Zapata, Tabasco, Mexico.
6. Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, United Kingdom.

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Denise Spaan

Instituto de Neuroetología, Universidad Veracruzana, Av. Dr. Luis Castelazo s/n, Col.

Industrial Animas, CP 91190, Xalapa, Veracruz, Mexico

denisespaan@hotmail.com

Tel. +52 2227188456

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.

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58 **Introduction**

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60   Line transect surveys are the most commonly used method to survey arboreal

61 primates (Peres, 1999; Buckland et al., 2010a, 2010b), providing abundance (hereafter

62 population density, e.g. individuals per km^2) or relative abundance estimates (hereafter

63 encounter rate, e.g. individuals per km), which form the base of a wide variety of studies in

64 ecology and conservation and aid in the formulation of species management plans. The

65 number of monkeys sighted may be affected by survey design, which in turn may affect

66 population density estimates or encounter rates.

67   Survey design is often limited by field conditions, but only a handful of studies have

68 investigated how survey design affects primate population estimates. Firstly, primate

69 surveys are commonly performed in the morning and late afternoon (Peres, 1999;

70 Ingberman et al., 2009) as primates are more likely to be encountered during periods of

71 heightened activity (Chapman et al., 1988; Peres, 1999), yet there is no general trend on

72 how time of day affects encounter rate or population density (Ingberman et al., 2009; Kun-

73 Rodrigues et al., 2013; Lee et al., 2014; Matsuda et al., 2016). For instance, early morning

74 is the optimum time to survey gibbons (*Hylobates agilis*; Lee et al., 2014), whereas time of

75 day did not affect either howler monkey (*Alouatta clamitans*) or sifakas (*Propithecus*

76 *coquereli*) population estimates (Ingberman et al., 2009; Kun-Rodrigues et al., 2013).

77 Secondly, the effects of survey speed on encounter rate remain poorly investigated (Shupe

78 et al., 1987; Iwanaga & Ferrari, 2002; Aliaga-Rossel et al., 2006; Nekaris et al., 2014),

79 despite its importance to detectability. Thirdly, line transect surveys are typically performed

80 by a group of one to two observers. Studies examining the effect of the number of

81 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 primary 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.

Method

Study site and subjects

115   We collected data between October 2014 and January 2015 in the Otoch Ma'ax

116   yetel Kooh 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 ±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 (±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 (χ^2=7.06, df=5, p=0.22) or excluding the time to

238   record individuals (χ^2=7.04, df=5, p=0.22). Similarly, the predictor variables did not affect

239   spider monkey subgroup counts including (χ^2=10.69, df=5, p=0.06) or excluding recording

240   time (χ^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 ± 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 disproportionally 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**

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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.