Shifting cultivation and hunting across the savanna-forest mosaic in the Gran Sabana, Venezuela: Facing changes

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Background. Human encroachment and overexploitation of natural resources in the Neotropics is constantly increasing. Indigenous communities all across the Amazon, are trapped between a population rise and a hot debate about the sustainability of hunting rates. The Garden Hunting hypothesis states that shifting cultivation schemes (conucos) used by Amazon indigenous communities may generate favorable conditions, increasing abundance of small and medium wildlife species close to the 'gardens' providing game for indigenous hunters.

Methods. Here, we combined camera trap surveys and spatially explicit interview dataset on Pemón indigenous hunting scope and occurrence in a mosaic of savanna and forest in the Gran Sabana, Venezuela to evaluate to what extent the wildlife resource use corresponds to Garden Hunting hypothesis. We applied Royle–Nichols model and binomial regression in order to: 1) assess whether abundance of small and medium wildlife species is higher close to conucos and 2) evaluate whether hunters select hunting localities based on accessibility to wildlife resources (closeness to conuco) more than wildlife abundance.

Results. We find mixed evidence supporting the Garden Hunting hypothesis predictions. Abundance of small and medium species was high close to conucos but the pattern was not statistically significant for most of them. Pemón seem to hunt in locations dominated by forest, where species abundance was predicted to be higher, than in close vicinity to conucos. Hunting scope was focused on the most abundant species located close to the conuco (*Cuniculus paca*), but also in less abundant and unavailable species (*Crax alector, Tapirus terrestris* and *Odocoileus virginianus)*.

Conclusions. Our research provided the first attempt of a systematic sampling survey in the Gran Sabana, generating a quantitative dataset that not only describes the current pattern of wildlife abundance, but sets the base-line to monitor temporal and spatial change in highland Amazon. We discuss the applicability of the estimates generated as a baseline as well as, environmental challenges imposed by economic, social and cultural changes such as mining encroachment for wildlife management.

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Abstract

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increasing. Indigenous communities all across the Amazon, are trapped between a population

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to the 'gardens' providing game for indigenous hunters.

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50 significant for most of them. Pemón seem to hunt in locations dominated by forest, where

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52 focused on the most abundant species located close to the conuco (*Cuniculus paca*), but also in

53 less abundant and unavailable species (*Crax alector, Tapirus terrestris*and *Odocoileus*

54 *virginianus)*.

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58 generating a quantitative dataset that not only describes the current pattern of wildlife abundance,

59 but sets the base-line to monitor temporal and spatial change in highland Amazon. We discuss

60 the applicability of the estimates generated as a baseline as well as, environmental challenges

61 imposed by economic, social and cultural changes such as mining encroachment for wildlife

62 management.

63

64 **Introduction**

65

66   Biodiversity loss has fueled a vigorous debate about sustainability of the current hunting

67 rates in the Neotropics and particularly in the Amazon basin (Robinson & Bennett, 2004; Lewis,

68 Edwards & Galbraith, 2015; Ripple et al., 2016; Benítez-López et al., 2017, 2019). Hunting by

69 inhabitants of tropical forests has increased in recent years (Fa, Peres & Meeuwig, 2002)☐ due

70 to human population growth, easier access to undisturbed forests, change in hunting technology,

71 scarcity of alternative protein sources, and higher demand for bushmeat (Bennett & Robinson,

72 2000; Benítez-López et al., 2017)☐. Worldwide, more than half of the intact forests and

73 wilderness areas are partially devoid of large mammals and birds, with a significant reduction in

74 abundance (Benítez-López et al., 2017, 2019)☐☐. However, current estimates of wildlife

75 abundance reduction do not take into account cultural factors such as taboos, religion, traditional

76 hunting technology, and prey preferences that can have a major influence in patterns of resource

77 use in indigenous communities (Vetter et al., 2011; Carvalho et al., 2015;; Gray, Bozigar &

78 Bilsborrow, 2015), which have a narrower hunting scope and magnitude compared with non-

79 indigenous hunters (Antunes et al., 2019)☐.

80

81   Biodiversity patterns in the Amazon have been altered by human societies since pre-

82 Columbian times (Etter, McAlpine & Possingham, 2008; Levis et al., 2017)☐, but the current

83 rate of transformation and loss are unprecedented and expected to increase in the future (Lewis,

84 Edwards & Galbraith, 2015; Jędrzejewski et al., 2017; Curtis et al., 2018; Ferrer-Paris et al.

85 2019)☐. Indigenous people in the Neotropics typically create forest-agricultural mosaics based

86 on shifting cultivation systems through clearing of small forest plots or "conucos" by slash-and-

87 burn practice (Warner, 1991)☐. The Garden Hunting hypothesis (Linares, 1976; Naughton-

88 Treves et al., 2003)☐ states that modification of plant community and *in situ* care of

89 domesticated plants in a shifting cultivation scheme, may generate favorable conditions (e.g.

90 high-nutrient, low-toxicity crops and the abundant browse of regenerating vegetation), for

91 adaptable, fast-reproducing species, such as rodents, peccaries, and armadillos (Constantino,

92 2019)☐, but in turn could act as population sink for large carnivores who are systematically

93 hunted when they venture close to the gardens (Naughton-Treves, 2002)☐. Interaction between

94 physical and cultural contexts influences the relationship with wild life species, either as a source

95 of protein, pest (Smith, 2005)☐ or pets (Naughton-Treves, 2002)☐☐. These local effects cascade

96 across the landscape, ultimately shape regional patterns of wildlife abundance and species

97 diversity that might range in effect from mild declines to more severe cases of "empty forests"

98 (Redford, 1992; Naughton-Treves et al., 2003; Smith, 2005; Constantino, 2015; Bogoni, Peres &

99 Ferraz, 2020)☐.

100

101   The Amazon basin still looks like an exceptional large region of intact forest, but in fact,

102 there are large regional differences in biodiversity patterns, cultural diversity and pressures on

103 natural resources (Naughton-Treves, 2002; ter Steege et al., 2020)☐. For example, the Guiana

104 Shield or highland Amazon has lower aboveground live biomass (Saatchi et al., 2007)☐,

105 anomalous savanna vegetation and forest-savanna mosaic (Rull et al., 2013)☐, nutrient

106 deficiency and low water retention capacity in soils than lowland Amazon (Dezzeo et al.,

107 2004)☐. Fauna and flora in highland Amazon show high diversity and endemism (Huber, Febres

108 & Arnal, 2001)☐, and lower prevalence of domesticated plants (Levis et al., 2017)☐. Low

109 human population density and limited agricultural potential of the lands in highland Amazon,

110 have prevented high rates of land cover change and infrastructure development, and relative

111 lower levels of threats (Rull et al., 2013; Ferrer-Paris et al. 2019)☐. While in lowland Amazon

112 the role and magnitude of external factors driving increasing hunting rates have been studied on

113 local and regional scale (Peres, 2000; Zapata-Ríos, Urgilés & Suárez, 2009; Constantino, 2015;

114 Gray, Bozigar & Bilsborrow, 2015)☐, these patterns remain understudied in the northern,

115 highland Amazon. This is particularly critical since prey abundance or density patterns in this

116 region are poorly known (Hollowell & Reynolds, 2005; Lim et al., 2005; Stachowicz et al.,

117 2020)☐. Indigenous communities in Latin and Central America obtain dietary protein mainly

118   through fishing and hunting (Bennett & Robinson, 2000), while shifting cultivation provides

119   them with vegetables, tubers, and some fruits (Rodríguez, 2004; Smith, 2005)□. Both activities,

120   shifting cultivation and hunting raise concerns about the sustainability harvest of natural

121   resources, especially because a transparent, legal framework for hunting is missing all across the

122   Amazon region (van Vliet et al., 2019)□.

123

124   Our study focused on Pemón indigenous communities, inhabiting a mosaic of savanna and

125   forest of the Gran Sabana in South Eastern Venezuela, highland Amazon. Extensive agriculture

126   and cattle raising activities are not viable in the Gran Sabana due to the scarcity of nutrients in

127   the soil (Rodríguez, 2004; Rull et al., 2013). Instead, Pemón indigenous communities practice

128   shifting cultivation, fishing and hunting (Coppens & Perera, 2008)□. They have cultural taboos

129   prohibiting hunting of certain wildlife (e.g. anteaters, foxes, armadillos, sloths, monkeys, and

130   felids such as jaguars and pumas) and preferences for hunting tapirs, deers, peccaries, pacas,

131   turtles and agoutis (Coppens & Perera, 2008). Additionally, new religion restriction has emerged

132   recently colliding with traditional customs (Knoop et al., 2020)□.

133

134   Here, we combine wildlife occurrence data from the first comprehensive camera-trap survey

135   in the Gran Sabana, and spatially explicit hunting information based on interviews with

136   indigenous communities in order to: 1) describe the Pemón's hunting practice, including scope,

137   occurrence and hunting technology, and 2) evaluate the influence of conucos on animal

138   abundance while controlling for the influence of habitat. Particularly we wanted to test two

139   predictions of the Garden Hunting hypothesis: a) abundance of small and medium wildlife

140   species is higher close to conucos, and b) hunters select hunting localities based on accessibility

141 to wildlife resource (closeness to conuco) more than wildlife abundance. To test the first

142 prediction, we fitted occupancy models (Royle & Nichols, 2003)☐ to predict relative abundance

143 of medium and small wildlife. For the second prediction, we related localities reported with and

144 without hunting by the interviewees, with variables explaining wildlife abundance and distance

145 to nearest conuco. We further compared the predicted abundance of wildlife in hunting and not

146 hunting sites. This study is intended as a baseline evaluation of wildlife presence under human

147 activity in a savanna-forest mosaic in highland Amazon. Although, our recommendations are

148 specific to our case study, our approach to combine different sources of hunting data and species

149 diversity may be widely applied in other regions (Huang et al., 2020)☐.

150

151 **Materials & Methods**

152

153 *Study area*

154

155   The study area covers 615 km² at the eastern part of the Gran Sabana on the border of

156 the Canaima National Park, with an elevation range 800 – 1200 m, close to the Venezuela –

157 Guyana international border (Fig. 1). Vegetation is dominated by scrub (*Clusia* spp. and

158 *Gongylolepis* spp.), broadleaf grassland and savannas of *Axonopus* spp. with scatter patches of

159 gallery forest (Huber, Febres & Arnal, 2001)☐. The Ilú and Tramén tepuis massif are surrounded

160 by continuous evergreen montane forest. Average temperatures are between 18 and 24°C and

161 total annual rainfall is 2000 – 3000 mm with a dry season (<60 mm / month) from December to

162 March (Rull et al., 2013). The Pemón are the only indigenous people inhabiting the Gran Sabana.

163 There are four communities within the study area: Kawi (1100 m; - 61.243 W; 5.451 N; 50

164 people 2016), Mare-Paru (884 m; - 61.184 W; 5.594 N; 45 people in 2016), Uroy-Uaray (1,093

165   m; - 61.232 W; 5.442 N; 150 people in 2016) and Wuarapata (896 m; - 61.157; W 5.512 N; 50

166   people in 2016; information about the number of inhabitants was obtained from community

167   leaders or *capitanes*).

168

169   *Hunting activity*

170

171   We used a direct, semi-structured interview approach to get information about hunting

172   and conuco occurrence within the six *blocks* (see *Sampling design and camera trap survey*

173   section) (Carvalho et al., 2015)☐. We used snowball sampling to identify interview participants.

174   Snowball sampling uses existing study subjects to recruit future subjects from among their

175   acquaintances (Voicu, 2011)☐. We initially identified five community leaders known to IS

176   (personal observation). These then contacted and recruited local hunters and farmers, and so on,

177   until we identified 29 people that were willing to be interviewed: three women and 26 men, all >

178   18 years old. All were indigenous from Wuarapata (11 people), Uroy-Uaray (8), Kawi (5) and

179   Mare-Paru (5) communities. Interviewees represented 10 % of the total population size and were

180   representative in terms of age distribution (mean 44 years old; 22 - 70 years old). The gender

181   unbalance in the sample likely reflects the role of male as spokesperson in their family group

182   (Coppens and Perera 2008).

183

184   All communities represented by their authority – *capitan* – agreed to participate in the

185   research and interview survey, as required by Venezuelan indigenous legislation (La Asamblea

186   Nacional de la Republica Bolivariana de Venezuela, 2005)☐. We obtained verbal informed

187   consent from each participant, after explaining research objectives and assuring participants that

188   information would be used only for research and presented in aggregate analyses, protecting each

189   participant's identity by assigning a numeric code to anonymize participants (Buppert &

190   McKeehan, 2013)☐. There was no compensation for participation. The questionnaire and

191   protocol were approved by Dr. Stanford Zent from the Human Ecology Laboratory of the

192   Venezuelan Institute of Scientific Research (July 2015), who acted as external ethical committee.

193

194   An interviewee was considered reliable if a participant could differentiate regional from

195   not-regional animals (e.g. *Tremarctos ornatus*) shown in pictures and drawings (plates of

196   Linares, 1998) and if the person has been living in the community on the Gran Sabana for most

197   of his/her life. We interviewed each participant independently to minimize biased responses

198   (Jones et al., 2008a)☐. We conducted the interviews in Spanish, using a local translator of

199   Arekuna Pemón's dialect when required, and registering the species' local name in Arekuna

200   Pemón's dialect.

201

202   We assumed that hunting trip was the main hunting method used (Urbina, 1979)☐, and

203   our interview survey focused on obtaining baseline information about three aspects of hunting

204   trip activity: (1) hunting occurrence; (2) hunting scope (which species are most important in term

205   of perceived value and preference); and (3) hunting technologies. We specifically asked about

206   the following topics: (1) whether they currently hunt or not in the vicinity of the conuco and

207   whether they did in the past; (2) the list of hunted species, both mammals and birds; (3) the three

208   most preferred hunted species, being the first species the most preferred; (4) preferred hunting

209   areas; (5) preferred hunting season; (6) occupation (mining, tourism, etc.); (7) food sources

210   (conuco, fishing and hunting, processed food); and (8) hunting technology used on hunting trips.

211   Besides direct questioning, we also evaluated hunting technology by reviewing the pictures from

212   the camera trap survey (see next section) looking for evidence of hunters, hunters with firearms

213   or dogs. In each sampling unit where the camera trap was installed, we asked whether they hunt

214   (1) or not (0) to obtain spatial distribution of hunting occurrence in the study area. To accurately

215   identify animals hunted, and avoid misinterpretation with animals' local names, we showed

216   pictures and illustrations of wildlife (Linares, 1998)□ to the participants.

217

218   To identify which species are important game species for Pemón people, we used two

219   criteria: the frequency a given species is reported as target game, and how frequently it is

220   mentioned as preferred game. For that we calculate two indexes for each species, importance of

221   hunting (Hv) and hunting preference (Pv) (Carvalho et al., 2015)□. Both indexes correct the bias

222   introduced by sampling size in the species citation rate, by multiplying the number of informants

223   giving information on each species. Hv is defined as:

224   Eq. 1 $Hv = \Sigma\left(\frac{h}{n}\right) x\ N,$

225   where h is the number of times a species is mentioned as a targeted animal, n the total number of

226   citations for all species, and N the number of interviewees

227   (Carvalho et al., 2015, modified from Phillips et al., 1994; Fernandes-Ferreira et al., 2012)□.

228

229   The hunting preference index (Pv), measure the frequency that each species is cited as the

230   first option for hunting among others, and is defined by:

231   Eq. 2 $Pv = \Sigma\left(\frac{p}{n}\right) x\ N,$

232   where p is the number of times a species is cited as the first option (among the three most

233   preferred hunted species), n the total number of citations for all prey species, and N the number

234   of interviewees. In this case, zero values (i.e. no preference) were excluded.

235

236   Due to the nature of the questions, the *Hv* and *Pv* should be interpreted as the perceived

237   importance and preference. Since we don't have counts of hunted individuals, we cannot

238   calculate frequency of hunting or consumption per species. We expect that the self-reported

239   species lists reflect those that are of highest valuable for Pemón people, but under some

240   circumstances the species consumed less frequently could be more reliably reported by recalls

241   (more memorable), than taxa that are consumed frequently (Golden et al 2013).

242

243   In some cases, Pemón names do not match scientific names and for example, they use

244   "savanna deer" or "forest deer" ambiguously for red brocket (*Mazama americana*) and gray

245   brocket *(Mazama gouazoubira),* and "armadillo" for the greater long-nosed armadillo (*Dasypus*

246   *kappleri*) and the nine-banded armadillo (*Dasypus novemcinctus*). So in these cases, the values

247   for *Hv* and *Pv* were calculated at genus level.

248

249   *Sampling design and camera trap survey*

250

251   We used data from a previous camera trap survey conducted between September 2015 –

252   April 2016. The original sampling design was developed to optimize covering habitat diversity in

253   order to evaluate how mammal species richness is related to habitat types, and is described in

254   detail in Stachowicz et al. (2020), but we provide here a brief summary of the initial setting and

255   how we adapted data *a posteriori* for our analysis. Sampling design comprised six 50 km^2 blocks

256   within the study area (B01 – B06). Blocks were selected to represent landscapes with different

257   configurations of forest, savanna and shrubs habitats. Since only 30 cameras were available,

258 sampling was divided into three periods of 60-days each, and in each period a two-levels

259 stratified random sampling was used to select 30 sampling units (five in each block) for camera

260 deployment. This stratification ensures a balanced representation of sampling units with different

261 coverage of habitat types and fragmentation in each block during each period. As a side effect of

262 this, some sampling units with unique values within each block (sites with high tree cover within

263 a block dominated by savanna) were selected for sampling in two or three periods and those

264 cameras were neither relocated nor replaced.

265

266   We also recorded direct observations and indirect evidence (scats, tracks, scratches on

267 trees, burrows, etc) of animal presence along the routes walked during field work, and recorded

268 their coordinates with GPS. We had a total of $n=159$ records during 29 days of camera

269 deployment and maintenance, with a mean of 16.8 km walked each day.

270

271   Total sampling effort was 4,548 cameras per day, which resulted in 771 detection events for

272 mammals and 226 events for birds across 60 camera sites (Table 1). Events represent sequences

273 of photos separated by less than 5 minutes and showing the same animal species and presumably

274 the same individuals. We identified mammal species (Eisenberg, 1989; Linares, 1998)□ and

275 birds (Hilty, Tudor & Gwynne, 2003)□ using reference works for Venezuela and South

276 America. We calculated the index of frequency of detection for all mammals and bird species

277 registered with camera traps as the number of detection events for species per 100 days of

278 camera trapping (O'Brien et al., 2010)□ in order to have available information to compare with

279 similar studies in Latin America.

280

281   *Predictive variables: Tree cover, distance to river and distance to conuco*

282

283   For this study, we calculated tree cover, distance to nearest conuco and river as covariates of

284   species abundance (Supplementary Material 1). Previous analysis suggested that most mammal

285   species in the study area are more associated with forest habitat than shrubs or savanna

286   (Stachowicz et al. 2020). We used mean tree cover (in percentage) as a quantitative variable

287   correlated with these habitat types and consistent with metrics used for the sampling design.

288   Mean tree cover was calculated from remote sensing products (Hansen MC et al., 2013)□ using

289   a 1 km buffer around the camera location *"tree_buffer."* This variable has a bimodal distribution

290   with a lower mode at 10-20% corresponding with the savanna, a higher mode at 70-80%

291   corresponding with forest, and intermediate values roughly corresponding with the less common

292   shrub habitat. We used 1 km radius under the assumption that it is wide enough to represent the

293   area of the most abundant game species home range (lowland paca *Cuniculus paca* 2 - 3 ha,

294   Jorge, M. & Peres, 2005; red-rumped agouti *Dasyprocta leporina* 3.4 - 1.6 ha, Benavides, Arce

295   & Pacheco, 2017)□ and narrow enough to maintain variability in tree cover within the scale of a

296   camera trapping site (Scotson et al., 2017)□.

297

298   Presence of rivers is considered an important variable explaining temporal and geographic

299   patterns of distribution and abundance of mammals (Constantino, 2015; Hedwig et al., 2018)□.

300   During the dry season when the camera traps were placed, access to water is an important

301   resource. We calculated distance to nearest rivers (in meters) using vector data of rivers (Señaris,

302   Lew & Lasso, 2009)□.

303

304   During fieldwork we marked with a GPS the location of active and recently abandoned

305   *conucos* (*n=25*) identified *in situ*, and hunting sites (*n=32*) reported by interviewees and

306   confirmed by the local guides (Fig. 1). Distance from each camera to the nearest conuco was

307   calculated using the GPS coordinates from cameras and conucos. This variable had an

308   asymmetric distribution with a mean value of 1.58 km and a range from 0 to 8 km. We also

309   recorded which cameras were located adjacent or near reported hunting sites (binomial variable

310   *hunting*, FALSE n = 23, TRUE n = 34).

311

312   After visual inspection of the distribution of tree cover, hunting occurrence, and distance to

313   conuco, we decided to discard three cameras with extreme distance values. We also discarded

314   four cameras that were active for less than seven days. Thus all following analyses count on data

315   from 54 cameras within 5 km of the nearest conuco, with more than seven days of activity (Fig.

316   2).

317

318   *Data analysis: Testing Garding Hunting predictions*

319

320   To evaluate the prediction of Garden Hunting Hypothesis we followed a three-step

321   approach using occupancy model, Chi-square test and logistic regression.

322

323   To test the prediction whether abundance of small and medium wildlife species is

324   higher close to conucos, we need a measure of influence of conucos while controlling for the

325   influence of habitat on species abundance, and the spatial and temporal heterogeneity in

326   probability of detection. For that, we fit a hierarchical Bernoulli/Poisson *N*-mixture model (Royle

327 & Nichols, 2003)□ for each species to evaluate how the probability of occupancy relates to tree

328 cover and distance to conuco, allowing for abundance-induced heterogeneity in detection

329 probability. These models are a type of latent abundance mixture models, and are often referred

330 as Royle–Nichols models, or RN-models. They are based on the assumption that the detection

331 probability at a survey point p_{ij} depends on the species' site-specific abundance N_i:

332 Eq. 4 $p_{ij} = 1\text{-} (1 - r_{ij})^{N_i}$,

333 where r_{ij} is the detection probability of a single individual. Repeated visits at a survey point

334 generate a history of detection/non-detection events y_{ij}, from which p_{ij} is estimated. The

335 abundance state (N_i) of site i was modeled as $N_i \sim$ Poison (λ_i), while the observation process was

336 modeled as $y_{ij}/N_i \sim$ Bernoulli (p_{ij}). Estimation of p_{ij} allows us to draw conclusions about N_i.

337   In order to build detection histories for species recorded during the camera trap survey,

338 we considered each camera location as a "site" (i; 54 in total). We divided the total sampling

339 period of 180 days into several ''visits'' (j). We tested different values of visit duration and

340 found that a duration of 21 days reduced the prevalence of zeroes but maintained enough number

341 of visits (three for each sampling period, up to nine for cameras fixed in the same location) to

342 successfully fit the model.

343

344   Covariates of N_i (site covariates) and p_{ij} (observation covariates) were modeled using the

345 logit link. We explored several covariates with alternative parameterizations to ensure best

346 possible model fit given the restricted sample size and low number of detection for some species

347 (see Supplementary Material 1 for details). As site covariates we used tree cover percentage

348 around the camera trap (*tree_buffer*), distance to river (*dist_river*), and distance to nearest

349 conuco (*dist_conuco*), all variables were standardized to zero mean and unit standard deviation.

350   Since a couple of species might be associated with shrub habitat with intermediate values of tree

351   cover (Stachowicz et al. 2020) we added a quadratic term (*tree_buffer²*) to their models.

352

353   We used sampling date, sampling effort (camera/day), and density of direct and indirect

354   off-camera records to account for spatial and temporal heterogeneity in detectability (Cubaynes

355   et al., 2010)☐. Sampling date (*date*) was recorded as the number of days since the start of

356   sampling (21 September 2015) to the beginning of the "visit" and standardized to zero mean and

357   unit standard deviation. Sampling effort (*effort*) was calculated as the number of days the camera

358   remained active divided by the duration of the visit. Thus, *effort* was always ≤ 1, and was set to

359   empty value (*NA)* when the camera was not present or inoperative during the whole duration of

360   the visit. We calculated tracks density (*track_dens*) as the inverse distance weighted sum of

361   wildlife activity recorded off-camera (direct observations and indirect evidence such as tracks,

362   scratches, cavities and excrement of animal presence during field-work):

363   Eq. 4 $track\_dens_i = \Sigma_{j=1}^{k} 1/d_{ij}^{q},$

364   where d_{ij} is the distance between camera *i* and record *j* for all *k = 159* records, and *q* is a fixed

365   power parameter that influences the degree of smoothing in the interpolation, we used *q = 0.25*

366   based on visual inspection. The result was standardized to zero mean and unit standard deviation.

367

368   For each species, we fitted a full model including the three observation covariates (*p*

369   (*date + effort + tracks_dens*)) and the three site covariates (λ (*tree_buffer + tree_buffer² +*

370   *dist_river + dist_conuco*)) using the *occuRN* function of the R package unmarked (Fiske &

371   Chandler, 2011)☐. We assessed model fit for the full model using goodness of fit test based on

372   Pearson χ^2 and parameter bootstrapping with 10,000 samples, and inspecting under- or

373   overdispersion ($\hat{c}$, calculated by dividing the observed χ^2 statistic by the mean of the statistics

374   obtained from bootstrap samples), magnitude of parameter estimates and standard errors, and

375   predicted values of the state variable at the sample locations (MacKenzie & Bailey, 2004; Royle,

376   2006)☐. For species with a suitable full model (with > 10 detections), we proceeded to create a

377   model selection table with all combinations of covariates (32 models for species with linear

378   effect of tree cover and 48 for species with quadratic effect of tree cover), ranked models

379   according to information criteria corrected for small sample size (AICc if $\hat{c} \leq 1$ or QAICc if $\hat{c} > 1$),

380   and the corresponding Δ(Q)AICc and model weights.

381

382   We assessed the relative importance of each detection and occupancy covariate by

383   calculating the sum of weights of the model containing that variable (Burnham, K.P. &

384   Anderson, 2002; Symonds & Moussalli, 2011)☐. Values range from zero to one indicating

385   increasing levels of support, and we use an informal scale to describe the level of support as very

386   strong (>0.9), strong (0.6 - 0.9), moderate (0.3 - 0.6) and low (<0.3). We further calculated

387   model averaged coefficients and predictions of the state variable (λ) based on the subset of

388   models with Δ(Q)AICc $\leq$ 10 (Burnham, Anderson & Huyvaert, 2011; Mazerolle, 2020)☐. In

389   case of overdispersion ($\hat{c} > 1$) we assumed the lack of fit is due to unaccounted sources of error

390   and used the value of $\hat{c}$ to inflate the standard errors and confidence intervals. For underdispersed

391   models ($\hat{c} \leq 1$), no modification to standard errors or intervals was made, but consider these as

392   conservative assessments of uncertainty (Kery & Royle 2015).

393

394   To evaluate the prediction whether hunters select hunting localities based on accessibility

395   to wildlife resources we first used the interview responses on vegetation type and season with

396   contingency tables, to evaluate which season and habitat type are used as hunting localities. For

397   that, we tabulated the number of interview responses from each community for the three levels of

398   preferred hunting vegetation types (forest, savanna and mixed) and the two levels of hunting

399   seasons (dry, and rainy season). We used the χ^2 (Chi-square) test to assess the significance of the

400   relationship between variables.

401

402   Second, we used the data collected during field work at 53 sites with cameras and fitted a

403   logistic regression to the binomial *hunting* variable with formula:

404   Eq 3 logit(*hunting)* ~ $\beta_0 + \beta_1$ *tree_buffer* + β_2 *dist_conuco* + β_3 *dist_river*

405

406   Third, we compared the prediction of latent abundance of the RN-models of each

407   species at these 53 sites, and compared values at sites with and without reported hunting .

408

409   *Ethical standards*

410

411   The study received permits from Ministerio del Poder Popular para Ecosocialismo y

412   Aguas 1419/3/33/2015 and Instituto Nacional de Parques (INPARQUES) 18/16 205, 156, 17 in

413   Venezuela, as well as from the indigenous authorities at each community. The instrument and

414   interview protocols used in Pemón communities were approved and widely used by Fundación la

415   Salle in Venezuela.

416

417   **Results**

418

419   *Frequency of detection of mammals and birds*

420

421   Camera traps detected a total of 25 species of mammals and 15 of birds of which four

422   species were detected once, seven were detected twice and the remaining 29 were detected three

423   times or more (Table 1, Fig. S1). The most frequently detected (FD) with high number of

424   detections events (D) mammals species were the lowland paca (FD = 5.38; D = 265), the red-

425   rumped agouti (FD = 4.2; D = 191), and the gray brocket (FD = 1.03; D = 47). Among birds, the

426   frey-fronted dove (*Leptotila rufaxilla*) (FD = 1.05; D = 68), and the black curassow (*Crax*

427   *alector*) (FD = 1.06; D = 48) were the most frequently detected (Table 1). The species with the

428   lowest frequency of detection were margay (*Leopardus wiedii*) (FD = 0.04 ; D = 2), the white-

429   lipped peccary (*Tayassu pecari*) (FD = 0.04; D = 2), collared peccary (*Pecari tajacu*) (FD =

430   0.04; D = 2), white-tailed deer *(Odocoileus virginianus*) (FD = 0.09; D = 4), Southern naked-

431   tailed armadillo (*Cabassous unicinctus*) (FD = 0.04 ; D = 2), common opossum (*Didelphis*

432   *marsupialis*) (FD = 0.04 ; D = 2), and capybara (*Hydrochoeris hydrochaeris*) (FD = 0.07 ; D = 3)

433   (Table 1). During the interviews with Pemón the majority of species registered by camera trap

434   were recognized, except margay and Southern naked-tailed armadillo, while giant armadillo

435   (*Priodontes maximus*) was only recognized by older interviewees.

436

437   *Hunting practice: Scope, occurrence, and hunting technology*

438

439   Of the 29 participants, 19 described themselves as active hunters, five as inactive hunters

440   who hunted in the past and five were no hunters (including the three women interviewed).

441   The most frequent food sources were agriculture (79%) and fishing and hunting (65%),

442   followed by consumption of processed food (51) (multiple choice was permitted). Only 14% of

443   interviewees identified hunting as an occupation that they carried out. Among other activities

444   carried out, almost all indicated agriculture (99%) and a large proportion indicated fishing

445   (86%), mining (37%), tourism (34%) and others (27%): handicrafts, raising of livestock and

446   transport (they could choose more than one activity). The majority of interviewees (79%),

447   reported that hunted meat was consumed within the family or the community. There was no

448   evidence of commercial hunting - sale of meat, leather or other products derived from the preys.

449

450   The most frequent hunting technology used during hunting trips was the shotgun (79%) (Fig.

451   3a and b), while traditional bow and arrows (6%; Fig. 3c), and sling to hunt the birds (10%; Fig.

452   3d) have recently gained importance due to limited availability of ammunition, 27%). The use of

453   dogs was not reported by interviewees but hunting dogs were visible in three out of nine events

454   of hunters detected by camera traps, where dogs accompanied armed people (Fig. 3a).

455

456   According to interviewees, at least nine species of mammals and three species of birds were

457   important game species for Pemón people (Table 2). We detected all of these species with the

458   camera trap survey (see below). The most important species (the highest Hv and Pv values; Table

459   2) were the white-tailed deer, lowland paca, and black curassows. Red-rumped agouti and South

460   American tapir (*Tapirus terrestris*) were also hunted, but were not mentioned as preferred game

461   (Table 2). Ten percent of interviewees reported that they only hunt and consume deer meat due

462   to religion restrictions.

463

464   *Occupancy models*

465

466   We explored latent abundance mixture model for 25 mammals and four bird species but

467   discarded models for species with poor fit (Supplementary Material 1 and 2). We completed

468   model selection and averaging for 12 mammal and three bird species with more than ten

469   detections and reasonably good fitting models. Among these 15 species, only ocelot (*Leopardus*

470   *pardalis*) ($\grave{c}$= 1.77) and nine-banded armadillo ($\grave{c}$= 1.29) showed sign of overdispersion (Table 3),

471   most species showed under-dispersion, with most values between 0.3 and 0.9 except the low

472   value for Great Tinamu (*Tinamus major*) ($\grave{c}$ = 0.21).

473

474   All variables received some degree of support for all species (Σ(Q)AICw > 0.23; Table 3).

475   Among the covariates of probability of detection, sampling effort had the highest level of support

476   in most species (six species with strong or very strong support, Table 3), except for *D.*

477   *imperfecta* (*track density* received most support), nine-banded armadillo (*date*), while three

478   species had similar low values for all three covariates (jaguar (*Panthera onca*), ocelot and great

479   tinamu; Table 3).

480

481   Among the covariates of lambda, tree cover had strong to very strong support for most of the

482   species except ocelot (moderate), giant anteater (*Myrmecophaga tridactyla*) (moderate) and

483   lowland paca *(low)*. For most species tree cover was modelled as a linear variable, except for

484   grey-fronted dove and tayra *(Eira barbara)*. Distance to conucos had only strong support for

485   tayra, lowland paca and black curassow, moderate support for two species and low support for

486   the rest (Table 3). While the distance to the river variable had high values for giant anteater and

487   jaguar*,* and low for the rest of the species.

488

489   Conditional model averages of the coefficient of distance to conuco was negative for most

490   species (higher estimates of latent abundance near to conucos) and close to zero or positive for

491   Guianan white-eared opossum (*Didelphis imperfecta*), great tinamou, crab-eating fox (*Cerdocyon*

492   *thous*), and black curassow (Fig. 4). However, the 95% confidence intervals of the estimates

493   overlap with zero, except for lowland paca, tayra, and black curassow.

494

495   In general, and despite few outliers, abundance predictions from the mixture models were

496   higher for most species in sites where the Pemón reported hunting activity (Fig. 5). This was true

497   for species with different values of hunting preference (*Hv*) and for species not mentioned as

498   important prey for Pemón, including carnivores (with the exception of crab-eating fox*;* Fig. 5).

499

500   *Selection of hunting localities*
501

502   Hunting occurrence in the study area was detected up to 5 km distance from conucos, both in

503   the savanna and forest (Fig. 2, Supplementary Material 1). Sampling units with reported hunting

504   activity were mostly located at 2.5 km from nearest conucos with tree cover > 40% (Fig. 2). Tree

505   cover (p = 0.006) and distance to rivers (p = 0.070) had a positive significant effect on the

506   hunting occurrence, but the effect of distance to conuco (p = 0.202) was negative and not

507   significant (Table 4).

508

509   Forest was the preferred hunting area for the majority of interviewees (72%), followed by

510   savanna (31%), and mixed forest – savanna areas (34%). This pattern was similar across

511   communities (χ^2 = 7.67; degree freedom = 6; p ≤ 0.263; Table 5). The majority of interviewees

512   hunt during the rainy season (68%), between May and August, while only 21% interviewees hunt

513   all year round, and 11% had not a preferred season to hunt. This pattern was similar across

514   communities ($\chi^2 = 9.89$; degree freedom = 6; p ≤ 0.129) (Table 5).

515

516   **Discussion**

517   A clear understanding of the relationship between human activities and wildlife

518   abundance patterns is crucial to identify the most appropriate conservation interventions in

519   complex landscapes with high biological and cultural diversity (Weinbaum et al., 2013; Gavin et

520   al., 2015)□. For the Gran Sabana and the Canaima National Park, despite their importance as

521   UNESCO World Heritage Site and the longstanding presence of Pemón people, base-line

522   knowledge about wildlife abundance patterns and how it changes across time, space, and as

523   response to human-based stressors is limited. Our research goes a step forward to fulfill these

524   gaps by providing the first attempt of a systematic sampling survey in the Gran Sabana,

525   generating a quantitative dataset that not only describes the current pattern of wildlife abundance,

526   but sets the base-line to monitor temporal and spatial changes. Further, to our knowledge, this

527   study is the first in providing quantitative and updated information about Pemón's hunting

528   occurrence, scope and practice, which has been poorly described across the highland Amazon

529   region. Last, but not less important, our hypothesis-based approach allowed us to go beyond a

530   list of species present and hunted, to try to shed light upon underlying patterns that can be better

531   integrated in programs for sustainable use of wildlife in accordance with the cultural and social

532   context. Finally, we place our research in the current social and economic situation of mining

533   encroachment in Guyana Shield.

534

535   *Current pattern of wildlife abundance*

536

537   The vegetation type had the most significant role explaining the abundance pattern of both

538   herbivores and carnivorous species in the study area (Table 3; Stachowicz et al., 2020). Most

539   species modeled, except the crab-eating fox, were more abundant in areas with higher cover

540   trees, which may correspond with forest and shrublands (Table 3). In the Gran Sabana, in

541   contrast to other Amazon areas, the savanna ecosystem is more prevalent than forest (Rull et al.

542   2013) thus, the observed higher abundance in forest and shrublands may reflect the patchy

543   distribution of resources (water, shelter and food) in the study area. Although hydric resources

544   had low importance for most modelled species, their inclusion significantly improved Royle-

545   Nichols model performance. In general, neotropical mammals shown higher richness in areas

546   close to water (Di Bitetti et al., 2008; Ferreguetti, Tomas & Bergallo, 2017)□. For example,

547   rivers and streams were important to explain abundance pattern for the jaguar (Table 3; Cullen et

548   al., 2013), that used to find their preys close to rivers (Weckel, Giuliano & Silver, 2006)□. Also,

549   for the giant anteater, gallery forests along river banks, provides refuge or escape routes from

550   fires (Diniz & Brito, 2013)□.

551

552   As expected, the medium and small species, with fast growing rates like the lowland paca

553   and the red-rumped agouti, had the highest frequency of detection (Table 1). The gray brocket,

554   although less frequent, was yet a prevalent species in the area, which contrast with the almost

555   absence of other deer species, the white-tailed deer (Table 1). Formerly widely distributed and

556   abundant, the white-tailed deer was only detected four times across the six survey months (Table

557   1). This low detection rate was unexpected because this species has a higher tolerance and

558   adaptation capacity to different habitats, than other ungulates such as peccaries and tapirs, being

559   detected even near human population centers (Gallina & Lopez Arevalo, 2016)□. Also, Pemón

560   refers that 10 years ago, the white-tailed deer used to be more abundant in the area (information

561   provided by interviewees). Although currently classified as Least Concern in the national

562   assessment of the Red List of Species (Rodríguez, Garcia-Rawlins & Rojas-Suárez, 2015)□, the

563   current low abundance of the white-tailed deer raised concern about their conservation status,

564   and highlight the need for an in-depth population and threats assessment in this area. Similarly,

565   the other threatened species detected (six Vulnerables and one Nearly Threatened) had also low

566   abundances. Among them, the black curassow and the great tinamou were important for Pemón

567   hunters, generating also concern about the population status in the future (Rios et al., 2020)□.

568

569   Evidence supporting the Garden Hunting prediction about higher abundance of small and

570   medium wildlife species close to conucos was not conclusive: Although most of the herbivorous

571   species modeled seem to have higher abundance close to conucos (Fig. 4) this effect was not

572   significant, and the only two species significantly attracted by conucos were tayra and lowland

573   paca. This pattern seems to agree with previous results on which tayra does not show a marked

574   preference for any type of habitat, while lowland paca showed significant preference to

575   shrublands or intermediate habitat, which likely correspond to conuco (Stachowicz, et al., 2020).

576

577   Among the species not attracted by conucos, black curassow was the only showing a

578   significant effect (Fig. 4), which contrasts with previous evidence in lowland Amazon and Piaroa

579   communities where cracids were observed within conucos in high abundance (Zent, 1997)□.

580   These difference might be due to different relationship between indigenous communities and

581   this bird species (with Piaroa using this species as a pet, while for Pemon is a game species), or

582   different habitat preferences of the species between lowland and highland Amazon. For other

583   species of curassow, the Endangered red-billed curassow (*Crax blumenbachii*), in Brazil was

584   more persistent in forest patches faraway from settlements, with hunting pressure potentially

585   exerting more influence on population persistence than habitat quality (Rios et al., 2020). Again,

586   more detailed population studies are required to better describe population status of this and

587   other endangered species in Gran Sabana, as well as improve our understanding of landscape

588   transformation and human activities in their population dynamics (BirdLife International, 2016).

589

590   *Pemón's hunting occurrence and practice*

591   We did not find support for the predictions of higher occurrence of hunting close to conucos

592   (Table 4). Pemón seem to hunt in locations dominated by forest (Table 4 and 5), where species

593   abundance was predicted to be higher (Fig. 5), than in close vicinity of conucos. To our

594   knowledge, there are no studies describing the size of Pemón hunting territories. Here, we found

595   that hunting activity was mostly focused on a radius of 2.5 km from conuco, but we have limited

596   data to test long range hunting (>5 km) (Fig. 2). Evidence from other Pemón community,

597   Tuauken located at ~ 30 km from study area, describes three types of hunting trips (Urbina,

598   1979)□: 1) hunting of large mammals such as tapirs and deer, implemented in a planned manner

599   by teams of many people, 2) hunting of smaller animals such as paca or aguti, implemented in a

600   semi-planned way by small teams and even by a single person, and 3) the informal, unplanned

601   hunts of turkeys and birds. The hunting detected in our research likely corresponds with the

602   second and third hunting types: small mammals and birds hunted in hunting trips performed

603   within short to medium distance from conuco.

604

605   Traps, incidental capture of game, and even the use of fire to capture deer and other large

606   prey species have been previously reported as hunting methods in Pemón communities (Bilbao,

607   Leal & Méndez, 2010; Sletto & Rodriguez, 2013)☐. However, during the 120 days of field work,

608   we did not detect traps, supporting the notion that traps are infrequently used by South American

609   indigenous communities (Dunn & Smith, 2011)☐. The use of dogs was registered on camera

610   traps but not mentioned by hunters during the interview. Literature indicates the presence of dogs

611   in hunting zones adjacent to the community, but hunters reported to kills the prey with a firearm,

612   not a dog (Dunn and Smith 2011). We compiled anecdotal information about incidental hunting,

613   mostly pigeons (grey-fronted dove), which were abundant in the study area (Table 1; Fig 5).

614   However, this activity was not even considered as hunting, diminishing it as part of kids games

615   and training (IS personal observation).

616   Hunting scope focused on the most abundant and easily accessible species, the lowland paca,

617   which was the most important hunting prey for Pemón people (Table 2). In lowland Venezuelan

618   Amazon, hunting scope of Ye'kwana and Sanema indigenous appears to be similar to those

619   observed by Pemón communities in this study: they hunt the most abundant mammals in the area

620   (the white-lipped peccary and the lowland paca; Castellanos, 2001; Ferrer et al., 2013)☐. In a

621   broader geographical context, this focus on high abundant and accessible species (usually pacas,

622   deers and peccaries) was also reported in indigenous communities in Panama (Smith, 2005)☐,

623   Honduras (Dunn & Smith, 2011)☐, in the Peruvian Amazon (Francesconi et al., 2018)☐, French

624   Guiana (Richard-Hansen et al., 2019)☐ and in Guiana (Roopsind et al., 2017)☐.

625   The fact that other less abundant or accessible species like the white-tailed deer and the

626   black curassow were identified as important prey for the Pemón, suggest that they practiced

627   selective hunting (Table 2). For the lowland paca with a high reproduction rate and short

628   gestation period (Grzimek, 2003a)□, this selective hunting may not translate into abundance

629   reduction. Indeed, this species has been considered as manioc and maize crop pest in Western

630   Brazilian Amazonia and Honduras (Abrahams, Peres & Costa, 2018)□. Nevertheless, in

631   Ecuadorian Amazon, abundance of lowland pacas, red brockets and collared peccaries have been

632   substantially reduced within a 3 km radius of the communities (Zapata-Ríos, Urgilés & Suárez,

633   2009)□ and 2 km in western Panama (Smith, 2008)□, raising concern about sustainability of

634   hunting. For the white-tailed deer, with lower reproductive rate and longer gestation period

635   (Grzimek, 2003b)□, this pressure likely had reduced their abundance: frequently hunted in the

636   last decade as source of animal protein and sport hunting (Danields, 1991; Gallina & Lopez

637   Arevalo, 2016)□, currently was scarcely reported as hunted. Our current dataset does not allow

638   us to discriminate whether the apparent reduction in abundance of the white-tailed deer is driven

639   by overhunting, demography, environmental or genetics factors (Madhusudan & Karanth, 2002;

640   Grzimek, 2003b)□. A sampling design surveying both locations with and without deer hunting

641   across different seasons, and taking into account spatial distribution of potential stressors, will

642   help understand the relative importance of hunting and other factors into deer abundance.

643   Interestingly, we did not detect reports of human – carnivore conflicts, even though

644   ocelot and tayra were detected close to conucos (Fig 4). Abundance of ocelot and jaguar were

645   predicted to be higher in Pemón's hunting locations (Fig. 5) suggesting potential competition for

646   prey resources between carnivorous and human. Our failure to find evidence of carnivore

647   poaching or conflict in Pemón communities may be a real pattern and not under-reporting

648   because: 1) in the Pemón communities people openly report hunting for other threatened species

649   such black curassows, 2) in other regions of Venezuela (even very close like Imataca), when a

650   poaching or conflict event exists, people freely exhibit felids skins at their houses as trophy hunts

651   and talk about the chasing of conflicting animals (IS *personal observation*), and 3) the cultural

652   taboo in Pemón people regarding hunting of carnivores (Coppens & Perera, 2008) seems to be

653   reinforced by more recently adopted religious which restrict the hunting scope only to deers

654   (Bonet, 2020; Knoop et al., 2020)□. However, under-reporting is still expected because of poor

655   recall capacity of interviewees. Clearly this topic requires a more in depth research, using

656   specialized questioning techniques widely applied to assess illegal wildlife trade and support

657   sensitive data collection (Nuno & St. John, 2014)□.

658   *The Garden Hunting hypothesis: current pattern of natural resource use*

659   Our results suggest that social-cultural context, and not only the surrounding environment,

660   determine where and what is hunted. Species attracted by the 'garden' such as lowland pacas,

661   red-rumped agouties and South American tapirs, were accessible and preferred prey (Fig. 4). In

662   contrast, other species similarly attracted to conucos such as the long-nosed armadillo and the

663   grey-fronted dove, were not preferred as hunting game (Table 2). This result contrasts with the

664   general notion that garden farmers often rely on game hunted in swidden gardens as a key source

665   of protein (Naughton-Treves, 2002)□, but agrees with more nuanced studies evaluating the use

666   and perception of wildlife in local communities in Peru, where 51% of interviewee considered

667   that the wildlife attracted to swiddens gardens bring no benefits for them (Naughton-Treves,

668   2002).

669   Pemón people traditionally had a very diffusely distributed population (Coppens &

670   Perera, 2008)□, with small and low densely populated settlements around which conucos were

671   cut in mature forest fragments adjacent to open savanna. In the last 30 years, Pemón

672   communities have become more permanent and bigger (Rull et al., 2013), resulting in a more

673   intensive land use (shorter than 5-26 years fallow periods that allows forest recovery; Kingsbury,

674   2001), and changes in the conuco locations. Again, there is no evidence of how settlement size

675   could affect hunting practices in Pemón communities. Several authors discuss how settlement

676   nucleation and sedentism around missions, along highways or tourist attractions has led to

677   localized game depletion in the Gran Sabana (Huber & Zent, 1985)□, but without supporting

678   data. Studies from other indigenous communities, the Piaroa, an indigenous group inhabiting in

679   the forested mountains of the Middle Orinoco, that were living in small, scattered, and highly

680   mobile communities until recently (Mansutti, 1990; Zent, 1992)□, suggest that increase in the

681   hunting size territory is not proportional to the increase in the population size (Freire, 2007)□.

682   However, Piaroa territories are bigger than those surveyed in the present study, and a study

683   covering a bigger area and more communities is necessary to evaluate the effect of settlement

684   size in hunting practices.

685   In general, Pemón practice seems to be sustainable but the perceived reduction in abundance

686   of important game species raises concerns for both livelihood sustainability and biodiversity

687   conservation. The general low impact of the current hunting pattern in the Gran Sabana could be

688   explained by their particular economic and cultural context. In the last decade frequency and

689   amount of hunting has been limited because of the high prices of cartridges. The lack of

690   ammunition forced the adoption of traditional, less effective hunting techniques such as bow –

691   arrows and sling, which only allow hunting for small prey and birds (Fig. 3c, d). As a result,

692   hunting has become more incidental, carried out only in special festivities. However, even with

693   cartridges, Pemón people seem to have relied more on conucos' production and fishing as

694   sources of protein, while hunting was a secondary source of protein (Urbina, 1979)□.

695   Additionally, protestant missionaries that have been present for more than a decade in the study

696   area, encourage indigenous communities to vegetarianism and quit hunting.

697

698   The new concern regards to creation of a large scale (12 000 km²) and extensive mining

699   development plan the Orinoco Mining Arc in 2016 (OMA; Lozada, 2019)□ in South of

700   Venezuela, which might change the current pattern of managing natural resources in the Gran

701   Sabana. It stands in non-compliance of environmental and indigenous social rights, increasing

702   the risk of pollution, and social and political conflict (Giordano et al., 2018)□ which likely could

703   increase demand for natural resources, including deforestation and over-hunting (Rodríguez,

704   2000)□. Already, in one of the studied communities, Uroy – Uaray, Pemón people have

705   extracted poor quality gold until 2012, and currently young men are leaving the community to

706   work in legal and illegal mines inside and outside of the Canaima National Park (SOS-Orinoco,

707   2018)□.

708

709   *Study limitations*

710   Carrying out field works in conflict zones such as Venezuela (Bull, 2020)□, requires

711   overcoming logistical challenges such as limitation of food and gasoline supply, distrust from

712   local communities, and constant presence of army and paramilitary, altogether impacting safety

713   of researchers and jeopardizing the time and geographical extent of the surveys (Gaynor et al.,

714   2016)□. This challenging social context, combined with budget limitations resulted in short

715   sampling effort, which was limited to six months in the dry season and limited number of

716   cameras. This likely impacted the statistical power of the analysis and limited our ability to

717   detect significant effects (Kery & Royle 2015). Although with this effort we were able to detect

718   82% of expected mammals species in the study area (Huber, Febres & Arnal, 2001; Stachowicz

719   et al., 2020), we failed to capture seasonal variations in abundance and occurrence of herbivores

720   and carnivores. For example, collared peccary and white-lipped peccary, were poorly detected

721   during the survey, likely because they perform seasonal movements during the dry season

722   (Keuroghlian, Eaton & Longland, 2004)□.

723   Although our sampling design optimized spatial coverage, we did not have enough

724   records (37% of species) to fit all species occupancy models. We found an important effect of

725   sampling effort on detectability of species (Table 3), but date of sampling was important only for

726   a few species. Pemón reported that the rainy season was their prefered season for hunting (Table

727   3), but our sampling survey covered only the dry season, thus we cannot compare how wildlife

728   abundance patterns change across the year (Ahumada, Hurtado & Lizcano, 2013)□. Increasing

729   sampling effort in both temporal and spatial scale, would allow us to get a better picture of their

730   dynamics and variability.

731   Although our interview sampling size was low, it represented 10% of the total

732   population size and was representative in terms of age distribution. However, low participation

733   in interviews among indigenous groups in Amazon is frequently reported (Knoop et al., 2020). In

734   any case, we are confident that concealment of hunting scope was low: People openly share

735   hunting reports for both threatened and not threatened species. This low level of concealment is

736   likely related to missing law enforcement protocols or tools to evaluate trends and magnitude of

737   wildlife use.

738   We were able to obtain spatial information of hunting activity in the study area, but a

739   longer presence of at least one year in the study area might assure higher interview success.

740   Extended survey time, combined with daily interviews approached, likely will result in a more

741   accurate and detailed description of hunting patterns (Jones et al., 2008b)☐, including quantities

742   of prey and frequency of hunting.

743   **Conclusions**

744   Large scale analysis of hunting rates might overlook the factors operating locally, such as

745   landscape type and matrix, wildlife diversity, cultural hunting taboos, religion, type of protein

746   sources (fishing, hunting), hunting technology, economic context or emerging threats, leading to

747   misinterpretations and incorrect management decisions. Understanding the relationship between

748   human activities and wildlife diversity patterns is crucial to identify the most appropriate

749   conservation interventions in complex landscapes with high biological and cultural diversity

750   (Weinbaum et al., 2013; Gavin et al., 2015; Rovero et al., 2020)☐.

751   Our study provides a baseline to evaluate the impact of the growing and accelerated threats

752   in the Gran Sabana ecosystem of highland Amazon. On one hand, the current level of shifting

753   cultivation practices seems to be sustainable and gives a room for sustainable agricultural

754   production in the long term. On the other, cultural transformations, migration of non-indigenous

755   groups for mining activity may possibly generate higher hunting activity. Update of the obsolete

756   legal framework and increased capacity for law enforcement regulating wildlife use will be

757   necessary to avoid local depletion of threatened and preferred prey species. Cost-efficient

758   monitoring strategies will be required to assess the effectiveness of the proposed conservation

759   actions. At regional scale, abundance of functional groups (Vetter et al., 2011; Mason &

760 Mouillot, 2013; Rovero et al., 2020)☐ may be used as an indicator of ecosystem functionality

761 (Ferrer-Paris et al. 2019). While, at the local scale the occurrence estimates provided by this and

762 similar studies (Stachowicz et al., 2020) can be used to calculate maximum sustainable offtake

763 quantitatively combine the supply and demand for wildlife resources (Robinson & Bennett,

764 2004)☐.

765

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769

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Table 1(on next page)

Nonvolant medium, large mammal and bird species detected during the camera trap survey.

Scientific, common names and names in Arekuna (Pemón dialect) are provided for each species. Frequency of detection index, total number of detections for species and survey method: are shown. CT = camera trapping, TRK= tracking, INT= interviews with local Pemón communities. IUCN Red List category based on country assessment (Rodríguez 2015) and dietary group based on Linares (1998) and Eisenberg (1989) are shown for mammals (herb – herbivorous, omni – omnivorous, carn – carnivorous and inse – insectivorous).

Common name	Scientific name	Species' name in Arekuna	Frequency of detection (FD)	Number of detection events (D)	Survey method	IUCN Red List Category	Dietary group
ARTIODACTYLA							
Red Brocket	*Mazama americana (Erxleben 1777)*	kutsari	0.44	20	**CT,TRK, INT**	**DD**	herb
Gray Brocket	*Mazama gouazoubira (G.Fischer 1814)*	kariyawku	1.03	47	**CT,TRK, INT**	**LC**	herb
White-tailed Deer	*Odocoileus virginianus (Zimmermann, 1780)*	waikín	0.09	4	**CT,TRK, INT**	**LC**	herb
Collared Peccary	*Pecari tajacu (Linnaeus 1758)*	poyinke	0.04	2	**CT,TRK, INT**	**LC**	omni
White-lipped Peccary	*Tayassu pecari (Link 1795)*	pakirá	0.04	2	**CT, INT**	**VU**	omni
CARNIVORA							
Margay	*Leopardus wiedii (Schinz 1821)*	-	0.04	2	**CT**	**VU**	carn
Ocelot	*Leopardus pardalis (Linnaeus 1758)*	kaukan	0.33	15	**CT,TRK, INT**	**LC**	carn
Jaguar	*Panthera onca (Linnaeus 1758)*	temenen	0.31	14	**CT,TRK, INT**	**VU**	carn
Puma	*Puma concolor (Linnaeus 1771)*	kusariwara	0.24	11	**CT,TRK, INT**	**LC**	carn
Crab-eating Fox	*Cerdocyon thous (Linnaeus, 1766)*	maikan	0.97	44	**CT,TRK, INT**	**LC**	omni
Tayra	*Eira barbara (Linnaeus 1758)*	yeruena	0.46	21	**CT, INT**	**LC**	carn
South American Coati	*Nasua nasua (Linnaeus 1766)*	kuachi	0.18	8	**CT, INT**	**LC**	omni
CINGULATA							
Greater Long-nosed Armadillo	*Dasypus kappleri (Krauss 1862)*	-	0.75	34	**CT, TRK**	**LC**	inse
Nine-banded Armadillo	*Dasypus novemcinctus (Linnaeus 1758)*	muruk	0.42	19	**CT,TRK, INT**	**LC**	inse
Southern Naked-Tailed Armadillo	*Cabassous unicinctus (Linnaeus 1758)*	-	0.04	2	**CT**	**LC**	inse

Giant Armadillo	*Priodontes maximus* (Kerr 1792)	mauraimu	0.18	8	**CT,TRK, INT**	**EN**	inse
PERISSODACYLA							
South American Tapir	*Tapirus terrestris* (Linnaeus 1758)	maikuri	0.31	14	**CT,TRK, INT**	**VU**	herb
DIDEPHIMORPHIA							
Guianan White-eared Opossum	*Didelphis imperfecta* (Mondolfi and Pérez-Hernandez 1984)	-	0.31	14	**CT**	**LC**	omni
Common Opossum	*Didelphis marsupialis* (Linnaeus 1758)	awaré	0.04	2	**CT, INT**	**LC**	omni
PILOSA							
Southern Tamandua	*Tamandua tetradactyla* (Linnaeus 1758)	woiwo	0.13	6	**CT, INT**	**LC**	omni
Giant Anteater	*Myrmecophaga tridactyla* (Linnaeus 1758	wareme	0.33	15	**CT,TRK, INT**	**VU**	insec
RODENTIA							
Lowland Paca	*Cuniculus paca* (Linnaeus 1766)	uraná	5.83	265	**CT,TRK, INT**	**LC**	herb
Red-rumped Agouti	*Dasyprocta leporina* (Linnaeus 1758)	akuri	4.2	191	**CT,TRK, INT**	**LC**	herb
Capybara	*Hydrochoeris hydrochaeris* (Linnaeus 1766)	parwena	0.07	3	**CT,TRK, INT**	**LC**	herb
PRIMATES							
Wedge-capped Capuchin	*Cebus olivaceus* (Schomburgk, 1848)	ibarakao	0.18	8	**CT,TRK, INT**	**LC**	omniv
Guyanan Red Howler	*Alouatta macconnelli** (Linnaeus 1766)	arauta	-	-	**TRK, INT**	**LC**	herb
BIRDS							
Pectoral sparrow	*Arremon taciturnus*		0.18	8	**CT, INT**	**LC**	
Savanna hawk	*Buteogallus meridionalis*	woroiwo	0.02	1	**CT, TRK,**	**LC**	

					INT	
Turkey vulture	*Cathartes aura*	kurüm	0.04	2	**CT, TRK, INT**	**LC**
Black curassow	*Crax alector*	pauwi	1.06	48	**CT, TRK, INT**	**VU**
Tinamous	*Crypturellus spp.*		0.04	2	**CT, TRK, INT**	
Variegated tinamou	*Crypturellus variegatus*		0.15	7	**CT**	**LC**
Little tinamou	*Crypturellus soui*	churima	0.24	11	**CT, INT**	**LC**
Ruddy quail-dove	*Geotrygon montana*		0.02	1	**CT**	**LC**
Grey-fronted dove	*Leptotila rufaxilla*	wakuma	1.5	68	**CT, TRK, INT**	**LC**
Green ibis	*Mesembrinibis cayennensis*		0.02	1	**CT, TRK, INT**	**LC**
Tropical mockingbird	*Mimus gilvus*	paraura	0.24	11	**CT**	**LC**
Rufous-winged ground cuckoo	*Neomorphus rufipennis*		0.02	1	**CT**	**LC**
Spix's guan	*Penelope jacquacu*	wora	0.18	8	**CT, TRK, INT**	**LC**
Great tinamou	*Tinamus major*	marú	0.53	24	**CT, TRK, INT**	**NT**
White-necked thrush	*Turdus albicollis*		0.73	33	**CT**	**LC**

1   * species documented only by vocalization and interviews with local communities.

Table 2(on next page)

Indices of hunting importance (Hv) and hunting preference (Pv) reported for the Pemón communities.

Mammal species are ordered by diet groups, birds are presented in one group as they have a mixed diet.

Diet group	Species	Common name	Hv	Pv	Red List of species
Mammals					
Insectivorous	*Dasypus kappleri* (Krauss, 1862)	greater long-nosed armadillo	0.244		LC
	Dasypus novemcinctus (Linnaeus, 1758)	nine-banded armadillo			LC
Omnivorous	*Tayassu pecari* (Link, 1795)	white-lipped peccary	0.975		VU
Herbivorous	*Tapirus terrestris* (Linnaeus, 1758)	South American tapir	2.681		VU
	Cuniculus paca (Linnaeus, 1766)	lowland paca	6.336	1.218	LC
	Dasyprocta leporina (Linnaeus, 1758)	red-rumped agouti	2.681		LC
	Odocoileus virginianus (Zimmermann, 1780)	white-tailed deer	6.823	4.874	LC
	Mazama americana (Erxleben, 1777),	red brocket	0.731		DD
	Mazama gouazoubira (G. Fischer, 1814)	gray brocket			LC
Birds					
	Tinamus major (Gmelin, 1789)	great tinamu	1.949		NT
	Crax alector (Linnaeus, 1766)	black curassow	4.630	0.975	VU
	Penelope jacquacu (*Spix, 1825*)	spix's guan	1.949		LC

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Table 3(on next page)

Model performance metrics.

The MacKenzie and Bailey (2004) test on the full model including goodness of fit test based on Pearson (χ^2), estimated dispersion parameter (c-hat) and significant level (*p*). The relative importance of each detection covariate is represented by the sum of AICc or QAICc weights (ΣAICw) of the model containing that variable. Variables with strong level of support (ΣAICw > 0.6) are in bold.

| Species | Total detections | MacKenzie and Bailey (2004) test on full model | | | Detectability | | | Lambda | | | |
		χ2	p	c-hat	*effort*	tracks_dens	*date*	tree_buffer	tree_buffer^2	dist_conuco	dist_river
Dasyprocta leporina	66	1093.79	0.715	0.521	**0.98**	0.42	0.29	**1.00**	-	0.31	0.43
Cuniculus paca	71	966.51	0.82	0.44	**0.97**	**0.92**	0.25	0.30	-	**0.87**	0.31
Leptotila rufaxilla	33	650.08	0.63	0.36	**1.00**	0.22	0.37	0.85	0.79	0.31	0.23
Cerdocyon thous	22	1217.31	0.44	0.59	0.42	0.26	0.23	0.54	-	0.31	0.31
Dasypus novemcinctus	17	956.26	0.14	1.29	0.22	0.23	**0.85**	0.41	-	0.32	0.23
Crax alector	31	1098.64	0.52	0.62	**0.73**	**0.71**	0.24	**0.98**	-	**0.64**	0.23
Leopardus pardalis	14	1427.13	0.13	**1.77**	0.24	0.25	0.23	0.35	-	0.26	0.26
Panthera onca	12	427.28	0.35	0.85	0.23	0.26	0.24	0.68	-	0.26	**0.68**
Dasypus kappleri	25	922.37	0.47	0.76	0.65	0.49	0.46	**1.00**	-	0.47	0.45
Mazama gouazoubira	33	846.97	0.65	0.52	**0.97**	0.22	0.22	**1.00**	-	0.57	0.30
Didelphis imperfecta	11	292.12	0.42	0.57	0.45	**0.96**	0.23	0.38	-	0.24	0.24
Tinamus major	18	319.06	0.91	0.21	0.23	0.29	0.24	**0.97**	-	0.25	0.24
Mazama americana	17	242.79	0.76	0.32	**1.00**	0.23	**0.88**	**0.98**	-	0.24	0.25
Myrmecophaga tridactyla	13	413.17	0.32	0.83	0.48	0.60	0.23	0.35	-	0.38	**0.89**
Eira barbara	16	282.14	0.70	0.41	0.24	0.22	0.23	**0.87**	0.23	**0.84**	0.24

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Table 4(on next page)

Regression coefficients (± SE) and standardized regression coefficient (z value) of each variable explaining hunting occurrence in the Gran Sabana

	Estimate	Standard error	z value	p
Intercept	-1.475	0.780	-1.890	0.05877.
tree_buffer	0.041	0.015	2.726	0.00641**
dist_river	0.001	0.000	1.812	0.06998.
dist_conuco	0.000	0.000	-1.276	0.202
Null deviance: 82.108 Residual deviance: 62.604 AIC: 70.604				
	Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1			

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Table 5(on next page)

The contingency tables showing preferences for habitat and hunting season among interviewees from the four Pemón communities.

Community	Habitat			Season		
	Forest	Savanna	Mixed	All year	Rainy season	No preference
Kami	4	1	2	1	2	1
Mare Paru	5	0	0	1	5	0
Uroy-Uaray	4	5	4	3	2	2
Wuarapata	8	3	4	1	10	0
	X2 = 7.6729	df = 6	p ≤ 0.263	X2 = 9.8886	df = 6	p ≤ 0.129

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Figure 1

Study area in the Gran Sabana, Venezuela showing location of the six blocks surveyed with camera traps and the location of conuco.
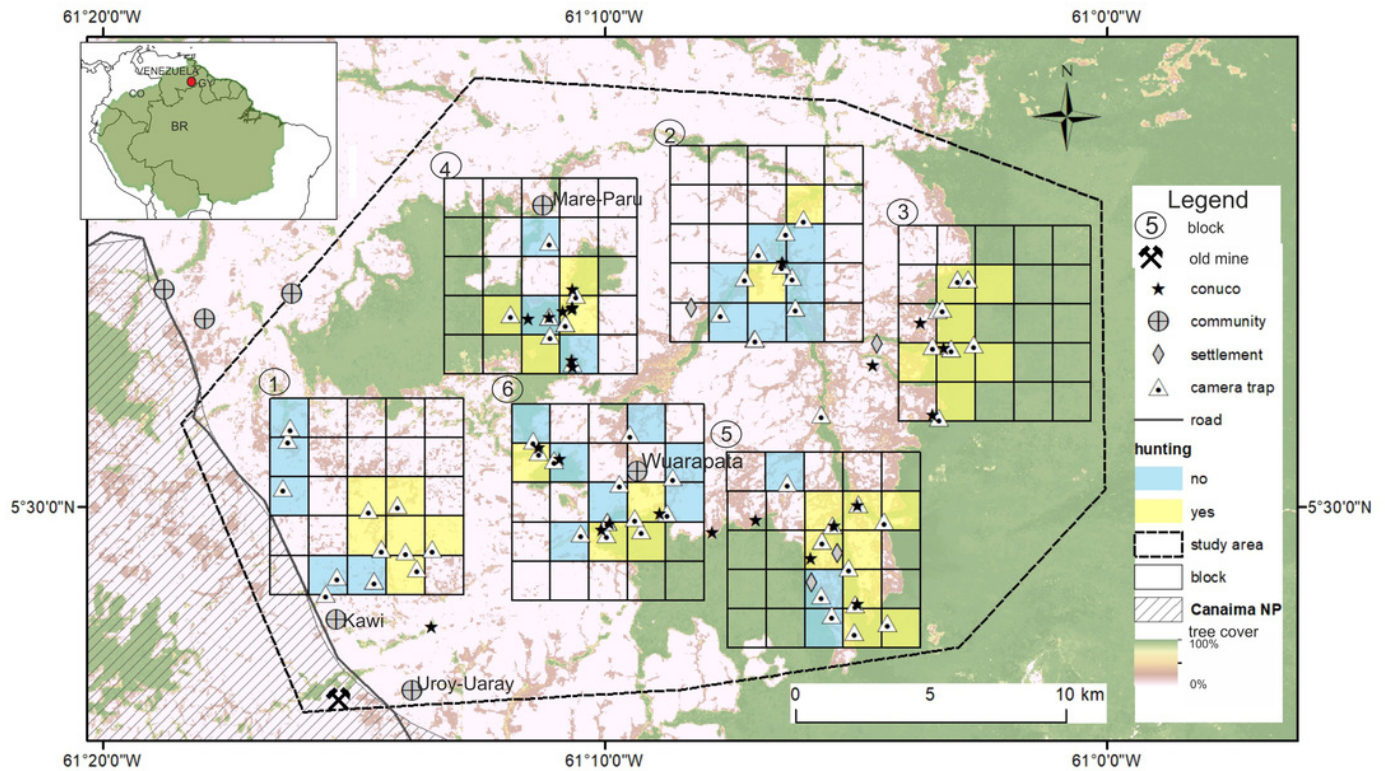
Figure 2

Distribution of predictive variables used to test the Garden Hunting hypothesis.

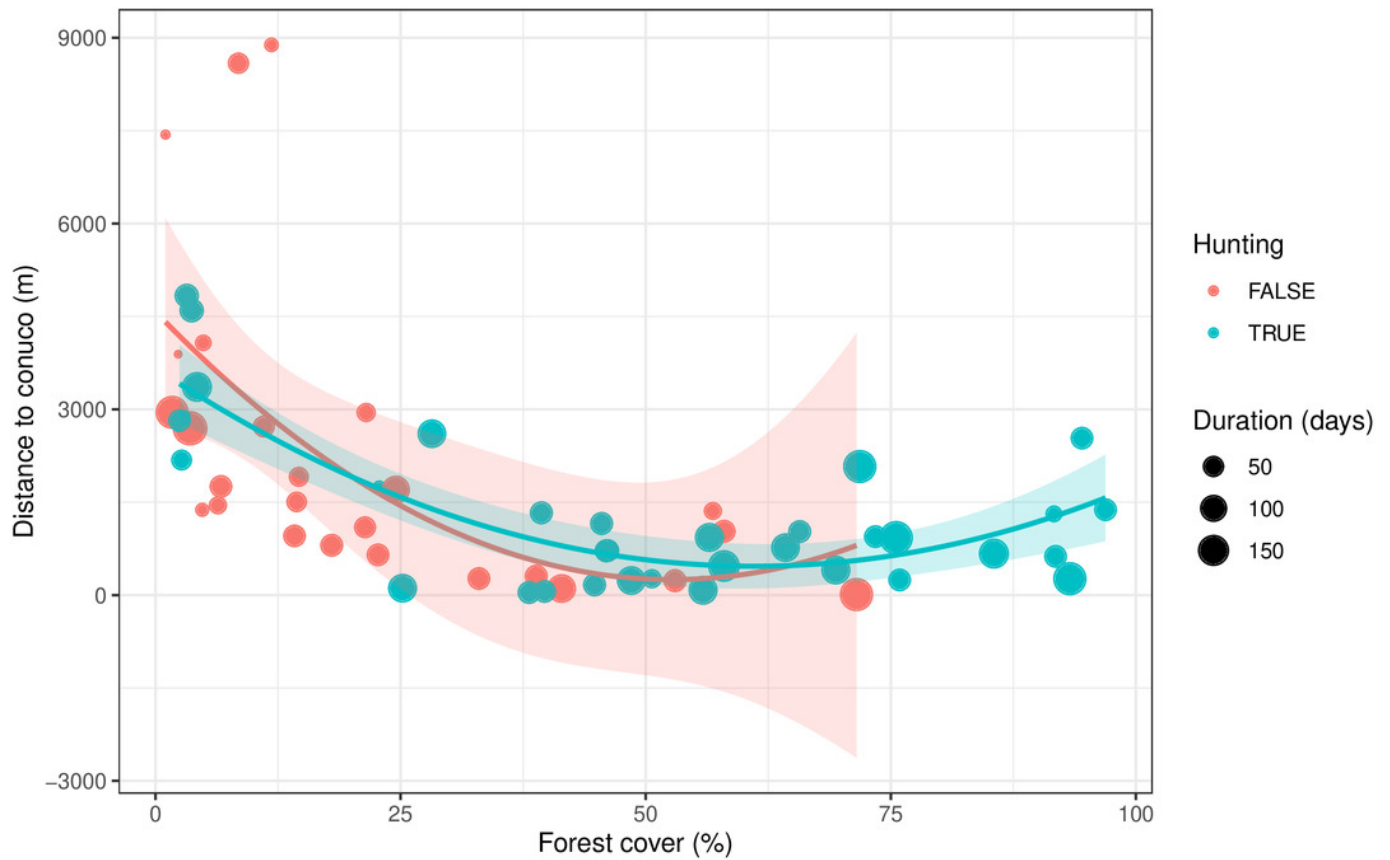Values of the percentage of tree cover, distance to conuco and hunting occurrence across sampling units is shown.

Figure 3

Hunting technologies used by Pemón.

a) hunter with a shotgun and dog captured by camera traps; b) hunter with a shotgun; c) hunter with a bow captured by camera traps, d) sling. Photo credit b) and d) Izabela Stachowicz.

Figure 4

Conditional RN-model averages of the coefficient of distance to conuco.

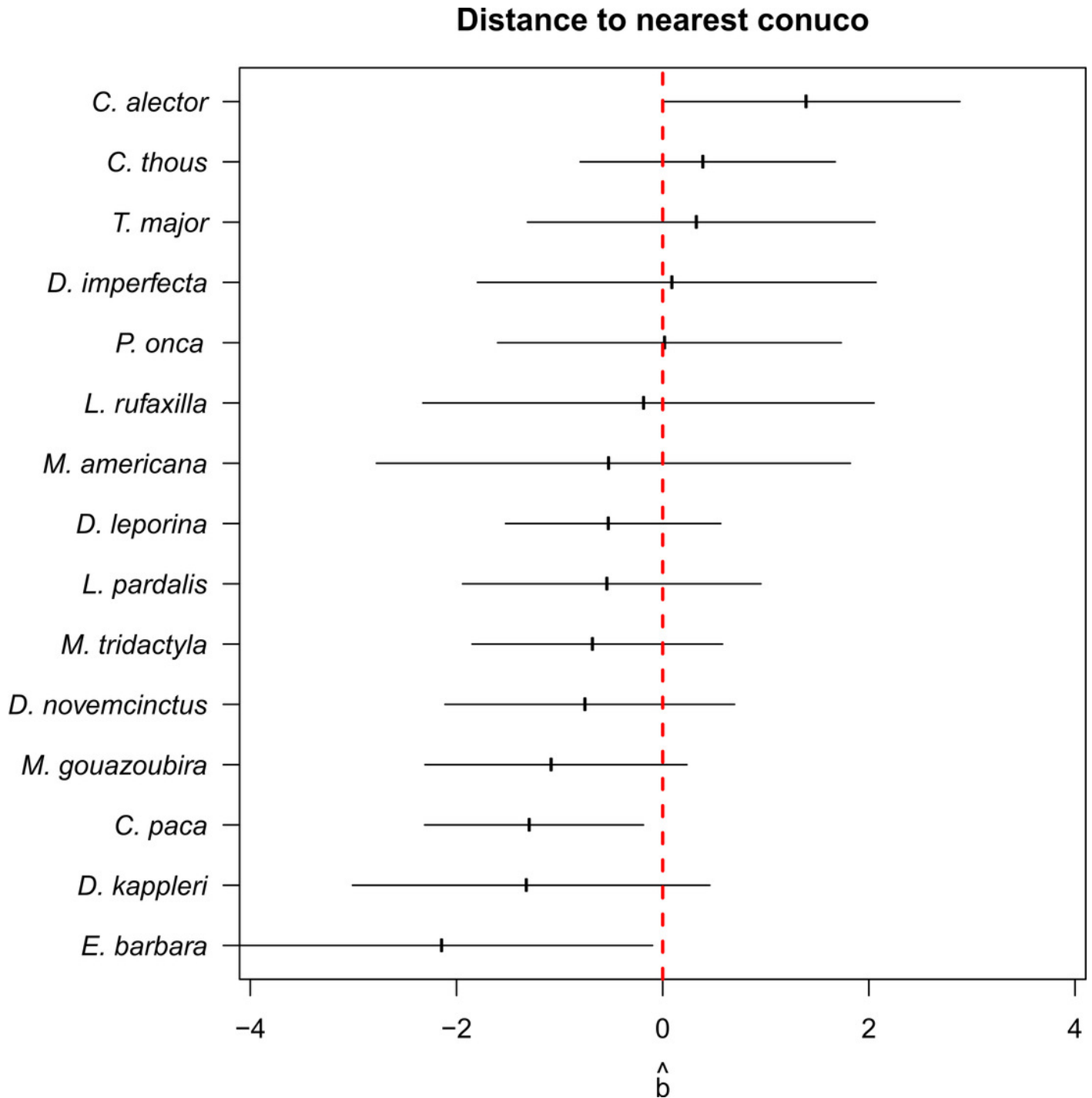Error bars are 95% confidence intervals.

Distance to nearest conuco

Figure 5

Predicted abundance over sampling units with and without hunting.

Species are ordered from left to right by decreasing *Hv* value, followed by species not reported as game.