1   Running title: Geoffroy's cat ecology in Brazil

2   **Density and spatio-temporal behaviour of Geoffroy's cats in a human-dominated**

3   **landscape of southern Brazil**

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48 **Abstract**

49 Geoffroy's cat is a small Neotropical felid, seemingly abundant throughout most of its
50 range and exhibiting considerable ecological plasticity. In Brazil, the species is
51 restricted to the Pampas, one of the most threatened biomes in the country, where
52 information on its ecology is scarce. Here we report the first assessments of its density,
53 habitat selection, and activity patterns in Brazil. The study was conducted in human-
54 dominated landscape at the extreme south of the country. Using Spatially Explicit
55 Capture-Recapture (SECR) analyses, the estimated population density ranged from
56 34.54 (±13.51 SE), based on camera trap and radio-telemetry data, to 41.78 (±16.12 SE)
57 individuals/100 km², based only on camera trap data. A Resource Selection Function
58 (RSF) analysis showed that our study population selected sites with native forest and
59 rivers, and avoided areas close to roads, which probably implies avoidance of human
60 contact. Although we observed a slight increase in its nocturnal activity during spring-
61 summer with respect to fall-winter, this population was predominantly nocturnal
62 throughout the year. The use of grasslands and croplands (non-protected areas) was
63 non-uniformly distributed through the hours of the day, whereas native forest was used
64 more uniformly.

65 Key words: Activity patterns; Brazilian Pampas; Habitat use; *Leopardus geoffroyi*;

66 Ranchlands.

67

68 **Introduction**

69

70 Behavioural and ecological features of a species influence its response to human

71 disturbance (Frid and Dill, 2002; Ciuti et al., 2012). While some species are driven to

72 extinction in human-dominated landscapes, others persist, raising the question of what

73 biological features underlie such discrepant outcomes. Geoffroy's cat (*Leopardus*

74 *geoffroyi*) is a small, solitary Neotropical felid categorized by the IUCN as "Least

75 Concern" (Pereira et al., 2015). This cat is considered abundant over most of its

76 distribution, ranging from Bolivia and southernmost Brazil to the southern tip of South

77 America (Macdonald and Loveridge, 2010; Cuyckens et al., 2016). Studies in

78 Argentina, the country occupying the largest proportion of its distribution, indicate that

79 Geoffroy's cat is tolerant of (and perhaps sometimes favoured by) habitat alteration and

80 can persist alongside livestock ranching and agriculture. This has led to the suggestion

81 that Geoffroy's cat is an ecologically adaptable species (Castillo et al., 2008; Pereira et

82 al., 2012; Pereira et al., 2015; Caruso et al., 2016). Testing this hypothesis using

83 multiple (and standardized) approaches, and at different field sites, is therefore

84 important to improve understanding of this species' ecology and its resilience to human-

85 induced disturbances.

86   Studies carried out in Bolivia, Argentina and Chile estimated very different

87 population densities at sites with contrasting ecological features (W. Johnson, personal

88 communication, in Nowell and Jackson, 1996; Cuellar et al., 2006; Pereira et al., 2011;

89 Caruso et al., 2012). Although some of these differences might be attributable to

90 different methodologies (such as different size of sample areas in capture-recapture

91 analysis), much of the intra-specific variation appears to reflect adaptation to contrasting

92 environmental factors, including human disturbance. There are no estimates of

93 population density of Geoffroy's cat throughout large areas of Paraguay, Uruguay and

94 Brazil, although it is usually considered abundant in Uruguay and Brazil (Soutullo et al.,

95 2010; T. Trigo, personal observation 2014, in Pereira et al., 2015). Insofar as most

96 previous studies of Geoffroy's cat population density used traditional capture-recapture

97 models, improved estimates can now be made using spatially-explicit capture-recapture

98 analysis (SECR: Royle et al., 2013; Efford, 2018). SECR models incorporate the spatial

99 information of captures, and resolve the "unknown sample area" problem.

100   Geoffroy's cats mostly occur in open landscapes. However, within these

101 landscapes, they can use open as well as closed habitats (Johnson and Franklin, 1991;

102 Manfredi et al., 2006; 2012; Pereira et al., 2006; Pereira et al., 2012, Caruso et al., 2016;

103 Castillo et al., 2019). Regarding activity patterns, this felid seems to be more

104 crepuscular and nocturnal than diurnal (Johnson and Franklin, 1991; Cuellar et al.,

105 2006; Manfredi et al., 2011; Pereira et al., 2011), although one report documents a

106   switch to diurnality in response to food shortage (Pereira, 2010). Taken together, these

107   observations suggest that Geoffroy's cat is flexible, and adaptable to diverse

108   environments, although many aspects of its ecology remain poorly known throughout

109   most of its range. To improve this knowledge and specifically to define the limits of its

110   intra-specific ecological variation, it is interesting to investigate in detail how

111   Geoffroy's cat behaves at the extremes of its geographical range.

112   The Brazilian Pampas is the only biome in Brazil where Geoffroy's cat occurs

113   (Pereira et al., 2015; Cuyckens et al., 2016), and has been categorized as a region with

114   medium-to-high predicted habitat suitability for this species (Cuyckens et al., 2016).

115   This region represents the north-eastern extreme of its range, and is thus an interesting

116   target for ecological research, but so far very few studies have investigated this species

117   in this area (Sousa and Bager, 2008; Trigo et al., 2013; Tirelli et al., 2018). In this

118   context, we aimed to estimate population density and to characterize behavioural

119   patterns of Geoffroy's cats in a human-dominated landscape typical of this region. More

120   broadly, we aimed to identify the factors underlying its apparent resilience (and

121   potential limits of that resilience) to anthropogenic habitat alterations.

122

123   **Material and methods**

124

125   *Study area*

126

127   The study was conducted from November 2013 to September 2015 in two

128   contiguous, private properties located in the Pampas ecosystem of southernmost Brazil

129   (30°04'S, 55°31'W). The study area covered ~30 km^2, and consisted of a mosaic of

130   natural habitat remnants, cattle pastures and croplands in the surroundings of a stream

131   ('Arroio Caverá') (Fig. 1). The native vegetation is characterized by a diversity of

132   grasslands (e.g., *Aristida murina* on shallow soils and *Paspalum notatum* on deeper

133   soils) (Boldrini, 2009) and by riparian forests adjacent to the stream, represented mainly

134   by *Sebastiania schottiana*, *Phyllantus sellowianus*, *Pouteria salicifolia* and *Syagrus*

135   *romanzoffiana* (Guadagnin et al., 2015). All riparian vegetation is included in legal

136   reserve and permanent preservation areas, which are areas instituted by the Brazilian

137   Forest code (Brazilian law 12.651/2012) determining the minimal percentage of native

138   vegetation that needs to be maintained in rural properties. These areas should be kept

139   free from cattle, but are sometimes impacted by incursions of livestock attempting to

140   access water. Cattle grazing is conducted on native grasses, and livestock management

141   practices are typical for the region, with ~90 cattle/ km², and husbandry activity (using

142   herding dogs) occurring during daytime, every day of the year (F. Tirelli, personal

143   observation, 2013-2015). Crops cover *ca.* 40% of the proprieties and comprise soybean,

144   rice, oat, and ryegrass. The annual rainfall averages 1500 mm, and the mean

145   temperature is 13°C in winter and 24°C in summer (Nimer, 1989).

146

147   *Camera Trapping*

148

149   Camera trap data were collected from November 2013 to September 2015, with

150   a gap in sampling between March and May 2014, as reported by Tirelli et al. (2018).

151   We employed 26 digital camera traps (20 Scout Guard[®], 4 Bushnell[®] and 2 Moultrie[®]),

152   which were positioned *ca.* 30 cm above the ground, with no lure. Cameras were active

153   24 hours per day on video mode (20 seconds), and were checked weekly to ensure

154   functionality. The total sampling effort was estimated by multiplying the number of

155   survey days by the number of functional camera traps per day.

156   Camera traps were preferentially placed in areas bearing evidence of felid

157   activity (tracks, faeces or radio-telemetry data). We employed two different camera trap

158   sampling protocols: (i) a camera trap layout aiming to collect data for density analysis,

159   used from January to August 2015 (we used two surveys of 48 days each to analyse

160   density), consisting of 13 stations, either inside or immediately outside the riparian

161   vegetation (Fig. 1), with paired cameras (to record both sides of an individual); and (ii)

162   for the remaining time of the study (2013-2014 and September 2015) cameras were

163   placed either individually or in pairs, covering a broader portion of the study area and

164   specifically aiming to collect data for the analysis of activity patterns. In every case, the

165   spacing between stations was maintained at ca. 600 m, the radius of the smallest home

166   range recorded for the species (Pereira et al., 2012).

167

168   *Live capture and radio telemetry monitoring*

169

170   Live captures and animal handling procedures were conducted under permit

171   SISBIO-36803, issued by the Brazilian Ministry of the Environment, and were carried

172   out at all times under the supervision of a veterinarian (see Tirelli et al. [2018] for

173   details on capture and radio-telemetry procedures). The study was also approved by the

174   university animal care and use ethics committee (PUCRS CEUA - 14/00400), and

175   followed the recommendations of the guidelines of the American Society of

176   Mammalogists, provided by Sikes et al. (2016).

177   All captured adult Geoffroy's cats were fitted with VHF radio-collars equipped

178   with activity and mortality sensors (Telonics; MOD-080-2) between May 2014 and

179   August 2015. Telemetry monitoring of these individuals was carried out from May 2014

180   to September 2015 at different times of the day, aiming to obtain at least three data

181 points (including location and activity) per individual in each 1-hr period within the 24-

182 hour cycle. For each data point, the spatial location of the individual was estimated by

183 triangulation, using at least three different bearings (taken at most 10 min apart) per

184 point. More information on this aspect of the methodology can be found in Tirelli et al.

185 (2018). Activity readings relied on the activity sensor built into each radio-collar, which

186 differentiated active (>43 beats per minute [BPM]) from non-active (≤43 BPM) states.

187 The threshold between the two states was defined empirically by cross-validation

188 between the activity reading and direct observation of individuals during this study. We

189 recorded the BPM of each individual every time a location bearing was collected, and

190 then calculated the average activity (in BPM) for that particular data point. This average

191 activity value indicated if the cat was active or non-active.

192

193 *Density estimates*

194

195 Two standardized survey periods were delimited from within our continuous

196 camera trapping sampling to estimate population density at our study site. One of them

197 targeted the summer (January and February 2015) and the other the winter (end of June

198 to the beginning of August 2015). Both periods were limited to 48 days to meet the

199 assumption of population closure (Balme et al., 2009). For this analysis, each camera

200 trap record was examined carefully and only those for which it was possible to discern

201 the spotting pattern on both flanks or on other body parts (e.g. forehead markings or tail

202 stripes) (Pereira et al., 2011) were retained in the dataset. These patterns were then

203 drawn, producing a reference database that was used for individual identification. To

204 maintain temporal independence between individual captures, each individual was

205 counted only once per camera station in a 24-hour period.

206   Density was estimated with SECR models (Royle et al., 2013), using the

207 package 'secr' (Efford, 2018) in R-3.2.3 (R Development Core Team, 2015). Because

208 this approach allows density to be estimated by combining different types of data

209 (Efford, 2018), we complemented our camera trapping records with animal locations

210 obtained by radio telemetry. We only included the telemetry data from individuals that

211 were monitored during the survey periods delimited for camera-trap sampling. Since

212 capture probabilities may be influenced by sex, age, and particular behavioural features,

213 we built six different models including combinations of these variables to represent

214 capture history, and tested their relative performances using the Akaike Information

215 Criterion (AIC) (Akaike, 1974). In addition, to allow direct comparisons between our

216 density estimates and others reported previously (Cuellar et al., 2006; Pereira et al.,

217 2011; Caruso et al., 2012), we also estimated population density using telemetry data

218 only (Benzaquín, 2008; Luengos Vidal et al., 2012), employing traditional Capture-

219 Recapture methods using MMDMOSA, MMDM, HMMDM, and home range (HR)

220 radius to estimate the size of the sampled area (Supplementary material S1).

221

222   *Resource selection functions (RSF)*

223

224   As variables for resource selection analysis, we assessed habitat composition,

225 distance to roads and distance to water (Supplementary material S6). We chose these

226 variables because the mosaic of habitat composition and roads are the main features of

227 the area, and water is often a crucial resource. To categorize habitat, we downloaded a

228 Landsat-7TM satellite image of the study site from the National Institute of Space

229 Research, Brazil (INPE), and used ArcGIS-10.4.1 (ESRI, 2016) to generate a

230 supervised classification of its habitats using a maximum likelihood approach (Patil et

231   al., 2012). We used the following three categories: native forest (NF), grassland (GS),

232   and cropland (CR). As for the other two variables, we downloaded shape files of the

233   road network and rivers from the Rio Grande do Sul (RS) state "Fundação Estadual de

234   Proteção Ambiental Henrique Luiz Roessler" (FEPAM). Subsequently, we used the

235   Euclidian distance tool in ArcGIS-10.4.1 to generate the maps of distances

236   (Supplementary material S6b and c).

237   The analyses of animal resource selection functions (RSF) were calculated based

238   on the locations of individuals obtained via telemetry. We computed the selection ratios

239   for 3rd order selection (Johnson, 1980). We used only this order because, according to

240   Walter and Fischer (2016), the use of the 2nd order selection in resource selection

241   analysis is necessary only across distinct landscapes. We calculated the extent of area

242   occupied by using a Minimum Convex Polygon 100% (MCP) for each individual using

243   the package 'adehabitatHR' (Calenge, 2006) in R software. Within each Geoffroy's cat

244   MCP, we compared the values of variables extracted from the locations of each animal

245   (resources used) with those of a random sample of 500 points (resources available)

246   (Walter and Fischer, 2016). We then used General Linear Models (GLM) by employing

247   the function *glmer* of the package 'lme4'1.1-17 (Bates et al., 2015) in R software. We

248   created nine distinct models including different combinations of the variables to

249   characterize the use of resources, and compared the models using the AIC. Finally, from

250   our top model, we created a map of predicted habitat suitability using 'adehabitatHS',

251   according to Walter and Fischer (2016).

252

253   *Activity patterns*

254

255   We investigated activity patterns using both camera trap and telemetry data. We

256   only included images obtained at least one hour apart from each other, which were then

257   assumed to represent independent events. We estimated activity patterns for each 1-hr

258   partition of the 24-hour cycle of the day, considering both the total survey period and

259   two separate seasonal partitions: spring-summer (October to March) and fall-winter

260   (April to September). These partitions were defined based on their distinct patterns of

261   sunrise and sunset at the study site during the survey period (Supplementary material

262   S5).

263   We used two analytical approaches for both the total survey period and seasonal

264   partitions: the Ridout and Linkie (2009) methods and Rayleigh's Uniformity test

265   (Fisher, 1993). We initially used the Ridout and Linkie (2009) methods to fit Von Mises

266   kernel density functions to times of observations of Geoffroy's cats in the total survey

267   period and in the seasonal partitions, and to estimate the coefficient of overlap (Δ_4)

268   between the two seasons (the coefficient ranges from 0 [no overlap in activity patterns]

269   to 1 [complete overlap]). These analyses were performed using the package 'overlap'

270   (Meredith and Ridout, 2014) in R-3.2.3. In addition, we used Rayleigh's Uniformity test

271   (implemented in the software Oriana-4.02 [Kovach, 2013]) to calculate the probability

272   of the null hypothesis that the data were distributed uniformly, for both the total survey

273   period and the seasons.

274   For the telemetry-based analyses, we considered the proportion of activity or

275   inactivity, which was obtained by dividing the number of 'active' or 'inactive' data

276   points by the total number of data points in each 1-h period. In this case, we only used

277   Rayleigh's Uniformity test, since the Ridout and Linkie (2009) methods are not

278   applicable to the proportional approach employed here.

279   To assess whether Geoffroy's cat activity was uniformly distributed throughout

280   the hours of the day in the different habitat types (NF, GS, CR), we used Rao's Spacing

281   Test (Kovach, 2013), and to test if activity patterns were significantly different among

282   habitats, we employed Watson's U^2 test (Kovach, 2013). For these analyses, we used

283   the software Oriana-4.02 and only telemetry data because our camera trap layout did not

284   sample the different habitat types equally.

285

286   **Results**

287

288   *Data collection*

289

290   The overall camera trap sampling effort in this study was 8,845 trap-days,

291   resulting in 522 felid images. Of these, 516 (98.85%) were Geoffroy's cats, two

292   (0.38%) were margays (*Leopardus wiedii*), and four (0.77%) were feral domestic cats

293   (*Felis catus*). In addition, 12 Geoffroy's cat individuals were live-captured, seven of

294   which (four males and three females) were radio-collared and monitored

295   (Supplementary material S2). The five additional individuals that were not monitored

296   included one cat that was killed by domestic dogs, one failed collar, and three

297   individuals that were captured in the last recapture campaign. Additionally, one of

298   female Geoffroy's cat died two months after its capture. We suspect that this female

299   was poisoned, because when we carried out a field necropsy, we found that its internal

300   organs were melted.

301

302   *Density*

303

304   The SECR density estimate was performed using two data sets ('camera trap

305   only' and 'combined', which used both camera trap and telemetry data) for two

306   different surveys (summer and winter). Each survey comprised 624 camera trap-days. In

307   the summer survey, we identified 11 different Geoffroy's cat individuals (four males

308   and seven females) in 49 independent camera trap captures. For five of them (three

309   males and two females), we obtained telemetry data (37 total points) that were

310   incorporated in the combined density estimates. In the winter survey, we recognized 11

311   distinct individuals (five males and six females) in 33 independent camera trap captures;

312   9 individuals (three males and six females) overlapped with those identified in the

313   summer. In this case, we could only include telemetry data from two females (17 total

314   points), which likely biased the combined density estimates for this season.

315   The trap-specific model (bk) (Table 1) provided the best fit for both types of

316   data in both surveys. The ΔAIC was >2 for the second most likely models in the

317   majority of cases, except for 'Winter combined' (Supplementary material S2). The

318   density estimates based on the SECR approach ranged from 34.5 to 41.78

319   individuals/100 km², and were extremely similar for the two seasons when using camera

320   trap data only (Table 1).

321   In addition to the SECR approach, we also estimated density using telemetry

322   data only, as well as traditional capture-recapture methods based on camera-trap or

323   combined data (see Supplementary material S1 for details). Most of these estimates

324   overlapped with those obtained with the SECR method, and provided a framework for

325   direct comparisons with results from previous studies (Table 2).

326

327   *Resource selection*

328

329   The RSFs were estimated using 434 telemetry locations from seven Geoffroy's

330   cats (four males and three females) (Supplementary aterial S3). The model with the best

331   AIC value included all three variables (native forest, distance to roads, and distance to

332   water [Table 3; Supplementary material S4]). Native forest and distance to roads

333   influenced the habitat use of Geoffroy's cats positively, whereas distance to water had a

334   negative effect (Table 3). The best model generated a map with greater habitat

335   suitability for areas in proximity to native forest and water (Fig. 2).

336

337   *Activity patterns*

338

339   The camera trap data set used to estimate activity patterns comprised 513

340   records. The data for the complete survey indicated that Geoffroy's cats were mostly

341   active during the night, with 71.6% of active observations between sunset and sunrise

342   (19:04 and 07:02, respectively) (Fig. 3). When the seasons were assessed separately

343   (240 records in summer-spring and 273 in fall-winter), cats were mostly active during

344   the night in summer-spring (78.8% of observations) and during nocturnal/crepuscular

345   hours in fall-winter (72.5% of observations) (Fig. 4). The intensity of activity decreased

346   before sunrise and increased before sunset in both seasons, although in summer the

347   nocturnal peak of activity was slightly higher than in winter. The coefficient of overlap

348   in activity patterns between seasons was $\Delta_4=0.79$ (CI 0.7-0.85) (Fig. 4). The mean

349   activity time *(*average $\pm$ SD) was 00:37$\pm$04:44 for spring-summer and 22:03 $\pm$ 06:56 for

350   fall-winter (Supplementary material S7). For all data sets, our results showed that the

351   activity patterns were not uniformly distributed throughout the day (Rayleigh's

352   Uniformity test: Z=20.97, P<0.01 for spring-summer; Z=3.72, P=0.02 for fall-winter).

353   We collected 751 telemetry fixes (263 active and 488 inactive) from 6 of the 7

354   collared cats (the activity sensor of one of the collars failed). Since only the active fixes

355   are informative for this analysis (which limited the available sample size), we

356   performed this estimate exclusively for the total survey period. Although some

357   differences in time-specific peaks are apparent between camera trapping and telemetry

358   data, both data sets indicated a similar mean time of activity for the survey period

359   (camera trapping: 23:36 ± 06:04; radio-tracking: 23:19 ± 03:47) and non-uniformity in

360   the use of the 24-hour cycle (Z=8.03, P<0.01 and Z=3.35, P=0.03, respectively; Fig. 5).

361   The proportion of active fixes was greater in NF (55%) than in CR (27%) and

362   GS (18%). Mean activity time in NF was 21:00 ± 02:16, while in GS was 04:00 ± 5:39

363   and in CR was 22:00 ± 01:39. Given the strong trend for predominantly nocturnal

364   activity in all three habitat types (NF: 59%; CR: 67.6%; GS: 60%), results of Watson's

365   pairwise test (which tests whether activity patterns differed between habitats) were non-

366   significant (NF *vs.* GS: U²=0.08, P>0.2; NF *vs.* CR: U²=0.02, P>0.5; CR *vs.* GS:

367   U²=0.06, P>0.5). However, when each habitat type was assessed separately, contrasting

368   patterns emerged, as the activity was significantly non-uniformly distributed throughout

369   the hours of the day in GS (Rao's Spacing Test; U=202.32, P<0.01) and CR (U=186.12,

370   P<0.05), whereas for NF the distribution was uniform (U=116.04, P>0.5)

371   (Supplementary material S8).

372

373   **Discussion**

374

375   Using a variety of methods to characterize Geoffroy's cat density, resource

376   selection and activity patterns in a human-dominated landscape, we found a population

377   at medium-to-high density, which concentrates its activity in the most preserved parts of

14

378   the study area and in the nocturnal hours. Density estimations for Geoffroy's cat have

379   ranged from seven (W. Johnson, personal communication, in Nowell and Jackson

380   [1996]) to 290 (Pereira et al., 2011) individuals/100 km². Our results indicate that

381   Geoffroy's cat in the Brazilian Pampas exhibit medium-to-high density when compared

382   to previously assessed populations, in agreement with Cuyckens et al. (2016), who

383   predicted a medium-to-high suitability for the species in the region. Our density

384   estimates using SECR approaches were similar to those reported by Caruso et al.'s

385   (2012) for an area with a similar habitat in Argentina. The landscapes of both study

386   areas were intensively modified by humans, and natural habitats were largely replaced

387   by cattle pastures and croplands. These alterations probably also influenced other

388   sympatric felid species. Only two of the seven felid species originally distributed in our

389   study area (Espinosa et al., 2017; IUCN, 2019) were recorded, and the margay was very

390   likely rare. A less diverse felid guild may reduce intraguild competition and release

391   resources that Geoffroy's cat can exploit to reach increased population densities. This is

392   in accordance with the hypothesis proposed by Cuyckens et al. (2016), that Geoffroy's

393   cat is probably expanding its geographical distribution into human-modified land, and

394   with the observation by Caruso et al. (2016) that this cat responded positively to the

395   degree of disturbance and fragmentation, possibly favoured by limited human

396   persecution.

397   However, there seems to be a limit to this adaptability (Castillo et al., 2008),

398   since totally open areas such as dry grasslands appear to be unsuitable (Caruso et al.,

399   2016; Manfredi et al., 2012). In this study, we observed that this Geoffroy's cat

400   population did not use environmental resources uniformly, selecting areas that were

401   more distant from roads and closer to water and native forest. Agreeing with Rytwinski

402   and Fahrig (2012), with respect to some mammals being most vulnerable to the negative

403   effects of roads, we suggest that the avoidance of areas close to roads by this Geoffroy's

404   cat population is related to human disturbance (including roads themselves and other

405   impacts that co-occur with them). The preference for covered habitats has been

406   described by other studies (Manfredi et al., 2006; 2012; Pereira et al., 2006; 2012;

407   Castillo et al., 2019), and is supported by our results. The significant and positive

408   relationship with water and native forest in the Brazilian pampas could be explained by

409   the resources and shelter provided by these habitats in this non-protected area. In

410   addition to the results on selectivity, we recorded videos with males and females

411   urinating and sniffing in riparian vegetation, supporting the idea of Manfredi et al.

412   (2006) and Soler et al. (2009), that wooded areas could also be used as 'communication

413   centres' in open landscapes. Finally, in the periods when this nocturnal felid was active

414   during the day the individuals mainly used native forest. This result supports the

415   hypothesis that these areas provide food and valuable shelter during daylight, and

416   indicate that legally preserved forested areas are essential for wildlife in this region,

417   highlighting the importance of enforcing their protection across this landscape in

418   southern Brazil.

419   In spite of some seasonal variation, possibly associated with fluctuations in

420   prey availability and/or preference (Pereira, 2010), during both seasons Geoffroy's cats

421   exhibited significantly nocturnal habits in our study area, as observed previously in the

422   Humid Pampas (Manfredi et al., 2011; Castillo et al., 2008), Low Monte-Espinal

423   (Pereira et al., 2011), Dry Chaco (Cuellar et al., 2006), and Magellanic subpolar forest

424   (Johnson and Franklin, 1991). Different sources of data (camera trap and telemetry)

425   consistently located the peak of activity around 23h, which supports the reliability of

426   this result. In short, Geoffroy's cats are nocturnal and crepuscular, with a seasonal

427   tendency to cathermerality.

428   Finally, the preference for 'natural' areas (native forest and water), the

429   avoidance of roads, and the essentially nocturnal habits (with diurnal activity limited to

430   native forest) in the Brazilian pampas are likely to be behavioural characteristics that

431   enable this small cat to persist, with a reasonably high population density, in a human-

432   dominated landscape in which other felids have already declined or disappeared

433   completely. Incorporating these findings into long-term conservation planning for this

434   region (e.g. maintaining or increasing areas of native vegetation interspersed among

435   human-altered habitats) should be relevant not only to ensure the persistence of

436   Geoffroy's cat, but also to maintain or restore other components of its native biota.

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439   **Acknowledgements**

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452   **References**

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618 **Table 1.** Capture probability, movement parameter (km), home range size (km²) and

619 population density estimation (obtained through Spatially Explicit capture-recapture

620 'SECR' models) of the best model (bk) assessed for Geoffroy's cats in the Brazilian

621 pampas. CT: camera trap data; TL: radiotelemetry data.

	Capture probability ($g0 \pm SE$)	Movement parameter ($\sigma \pm SE$)	Home range size[a] (average $\pm$ SD)	Density (Individuals per 100 km² $\pm$ SE)
Summer	0.03 ± 0.01	0.88 ± 0.15	-	41.78 ± 16.12
Winter	0.01 ± 0.01	1.05 ± 0.24	-	41.44 ± 19.20
Summer (CT+TL)	0.02 ± 0.01	-	3.53 ± 3.2	34.54 ± 13.51
Winter (CT+TL)	0.02 ± 0.01	-	1.24 ± 0.83	63.2 ± 24.77[b]

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623 [a] Estimated by MCP 100%.
624 [b] These results were likely biased by telemetry data that included only two females.
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641 **Table 2.** Comparison of density estimates (individuals/100 km²) for Geoffroy's cat obtained in this study with those reported previously for other

642 areas.

	Present study	Nowell and Jackson 1996[d]	Cuellar et al. 2006	Pereira et al. 2011		Caruso et al. 2012
Location	Privately owned areas	Torres Del Paine National Park	Kaa-Iya del Gran Chaco National Park	Lihue Calel National Park	Privately owned areas	Privately owned areas
Ecoregion	Uruguayan Savannah	Magellanic subpolar forest	Dry Chaco	Low Monte-Espinal		Espinal
Country	Brazil	Chile	Bolivia	Argentina		Argentina
Human impact[a]	medium	low	Low	low	high	medium
Other felids recorded	Margay, feral cats (rare)	Puma	Jaguar, puma, jaguarundi, ocelot, margay	Pampas cat and jaguarundi (rare)	none	Pampas cat
Suitability[b]	0.25-0.50	0.25-0.50	0.25-0.50	>0.50		>0.50
Density estimates						
SECR (CT+ Telemetry)	34.54 (16.48 – 72.37) and 63.22 (30.14 – 132.58)[c]	-	-	-	-	-
SECR (CT only)	41.78 (20.14 – 86.70) and 41.44 (17.46 – 98.36)	-	-	-	-	45 (22.95-88.28)
Telemetry only	32.91	7 - 12	-	-	-	50.22
MMDMOSA	32.44 (32.44 – 36.05) and 43.25 (43.25 – 108.15)	-	-	-	-	-
HR radius	51.16 (51.16 – 56.85) and 68.22 (68.22 –170.553)	-	-	140 (94-274)	240 (189-321) and 230 (155-374)	21.94 (21.94 - 60.31)
MMDM	38.05(38.05 – 42.281) and 50.74 (50.74 – 126.85)	-	-	100 (66-191)	120 (98-167) and 160 (109-262)	16.21 (16.21-44.56)
HMMDM	87.89 (87.89 – 97.65) and 117.18 (117.18 – 292.97)	-	9.52 - 42.11	190 (122-355)	220 (170-290) and 290 (197-473)	24.18 (24.18-66.50)

643
644 [a] Definition: low (reserve areas), medium (farmlands with 20-100 cattle/km²[Robinson et al.(2014)]), high (farmlands >100 cattle/km²[Robinson et al.(2014)]).
645 [b] Extracted from Cuyckens et al. (2016);
646 [c] In winter we could only include telemetry data from two females which likely biased the combined density estimates.
647 [d] W. Johnson, personal communication, in Nowell and Jackson (1996).

Table 3. Resource selection function analysis using General Linear Models for intra-populations of radio-tracked Geoffroy's cats in the Brazilian pampas using three different variables: habitat composition, distance to roads and distance to water. SE=standard error, LL= lower limit, UL=upper limit

	Estimate	SE	LL	UL	Z-value	P-value
Native forest	0.35	0.16	0.04	0.67	2.23	0.02 *
Grassland	-0.04	0.13	-0.29	0.23	-0.27	0.79
Distance to roads	0	0	0	0	3.95	7.92e-05 ***
Distance to water	0	0	0	0	-4.98	6.26e-07 ***

Note: The 'cropland' of the 'habitat composition' variable is omitted, since 'habitat composition' is a categorical variable, which is converted into a 'dummy variable' In GLM, one of the levels is used as a reference; in this case it was 'cropland'.
Significance codes: 0 '***', 0.001 '**' ,0.01 '*', 0.05 '.' ,0.1, ' ' 1

Figure Captions

Fig. 1. Location of the study site in southernmost Brazil, along with a characterization of its habitat composition (NF – Native forest, CR – Cropland, GR – Grassland), camera trap layout (black hexagons) and telemetry relocations (white circles) of radio-collared Geoffroy's cats. Coordinate system: UTM Zone 21J.

Fig. 2. Map of the study site showing Resource Selection Functions (RSF) with prediction classes based on data from telemetry relocations of radio-collared Geoffroy's cats and from variables of habitat composition, distance to roads and distance to water. Coordinate system: UTM Zone 21J.

Fig. 3. Kernel-density estimates of the daily activity patterns of Geoffroy's cat in the Brazilian pampas based on camera trap data. The short vertical lines above the x-axis indicate the times of individual photographs (n=513) and the black solid vertical lines indicate the mean time of sunrise (07:02) and sunset (19:04) across the whole year (Supplementary material S5).

Fig. 4. Kernel-density estimates for activity patterns of Geoffroy's cats in the Brazilian pampas based on camera trap data in summer (n=240) and winter (n=273). The solid and dashed vertical lines indicate the mean time of sunrise and sunset in summer (06:57 and 20:03) and winter (07:15 and 18:10), respectively (Supplementary material S5).

Fig. 5. Circadian activity patterns of Geoffroy's cat in the Brazilian pampas. Bars indicate the proportion of active records with respect to the total number of fixes (in the case of telemetry data) and of records taken (for camera trap data) at that hour of the day. Grey line is the Standard deviation ellipse. (a) Telemetry data (n=751 fixes from 6 individuals). (b) Camera trapping data (n=513 photos).

Supplemental materials

Supplementary material S1. Capture-Recapture methods to estimate density.

Supplementary material S2. Density estimation models ('secr' package [Efford 2018] in R) and their corresponding AIC values for two surveys, including analyses with only camera-trap data (summer and winter) and camera-trap data combined with telemetry data (summer combined and winter combined). Parameters include: predictor variables[a], g0 = baseline detection, sigma = scale parameter. Additionally, P= Parameters; logLik = strength of evidence of each model; AICc = AIC with small sample bias adjustment, ΔAICc = difference between AICc model and the best model; AICcwt = weight attributed to each model.

Supplementary material S3. Estimation of habitat available area for each individual using Minimum Convex Polygon 100% (MCP) from Tirelli et al. (2018).

Supplementary material S4. General Linear Models ('lme4' package (Bates et al., 2015) in R) and their corresponding AIC values. BIC= Bayesian information criterion; logLik = strength of evidence of each model; deviance=measure of goodness of fit; df.resid =residual degrees-of-freedom.

Supplementary material S5. Mean and standard deviation for time of sunrise, time of sunset and duration of daylight collected during the entire study period of study and divided between two seasons; data obtained for the Alegrete municipality (which includes most of our study site), RS, Brazil.

Supplementary material S6. Variables used in Resource Selection Function analyses performed in this study. a) Habitat composition (with three categories: native forest, grassland and cropland). b) Distance to road (meters). c) Distance to water (meters). Coordinate system UTM Zone 21J.

Supplementary material S7. Seasonal activity patterns of Geoffroy's cats in the Brazilian pampas in two different seasons. Bars indicate the proportion of camera trap records taken at that hour of the day. Grey line is the Standard deviation ellipse. A. Spring-summer (n=240). B. Fall-winter (n=273).

Supplementary material S8. Circadian activity patterns of Geoffroy's cat in the Brazilian pampas in three different habitats: A. native forest, B. croplands, and C. grasslands. Bars indicate the proportion of active records with respect to the total number of fixes at that hour of the day. Arrow represents the mean time of activity.

Supplementary material S1. Capture-Recapture methods to estimate density

Material and Methods

Traditional Capture-Recapture methods were used here to compare our results with those reported by other density studies. First, we estimated abundance (*N*) model results for both survey periods (summer and winter); this was carried out in the software CAPTURE (Rexstad & Burnham, 1991), and we selected the best model using the model selection criteria (based on a goodness-of-fit test) with same software (Otis, 1978). Second, we calculated the area effectively sampled (*AES*) applying four different approaches of buffer-width estimation: 1) mean maximum distance moved by individuals outside the area delineated by the outer traps (MMDMOSA); 2) mean maximum distance moved (MMDM); 3) half mean maximum distance moved (HMMDM) (Balme *et al*., 2009); and 4) the radius of the mean adult home-range size of the studied population (HR radius) (Pereira *et al.* 2011). The estimations were computed for the Geoffroy's cats living in the area. Third, we calculated density by dividing *N* of each survey period by the values of *AES* generated from with method. Density was also estimated by the telemetry data only; to do so, we assessed the HR of radio-collared individuals with the 95% kernel approach; home range overlaps were then corrected and the total area occupied by monitored cats was calculated (Caruso *et al*., 2012). Finally, the total number of individuals monitored was divided by the estimated *AES*. All *AES* analyses were calculated using ArcGIS 10.4.1 (ESRI, 2016).

Results

The best models to explain the capture and recapture of the species were $M(0) = 0.95$ and $M(h) = 1.00$ in the summer and $M(0) = 1.00$ and $M(h) = 0.91$ in the winter. White *et al*. (1982) suggested precaution in the use of the null model, $M(0)$, especially in a situation that includes a small sample size or possibility of individual heterogeneity.

Therefore, here we used the M(h) model, which assumes heterogeneity among individuals in their capture probabilities (White et al. 1982). Our sampling structure was not validated for the closure test provided by CAPTURE; as our surveys were performed in 48 days, we assumed no change in the population during these periods (Pereira *et al.* 2011; Caruso *et al*. 2012). The capture probability using CAPTURE was 0.09 for summer and 0.05 for winter, and the abundance was 09 (± 1.98 *SE*) for summer (*CI* 7-10) and 12 (± 3.02 *SE*) for winter (*CI* 12-30). By using MMDMOSA (1.73 km ± 0.83) the *AES* was 27.74 km²; with MMDM (1.52 km ± 0.88 *SD*) the *AES* was 23.65 km²; by using HMMDM (0.76 km ± 0.44 *SD*) it was 10.24 km²; and with HR radius the total sample area was 17.59 km². Finally, from the seven radio-collared Geoffroy's cat HRs, the total sampled area with telemetry was 21.27 km². All density estimations were than calculated (Table 2).

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Supplementary material S2. Density estimation models ('secr' package (Efford 2018) in R) and their corresponding AIC values to two surveys for analyses using only camera trap data (summer and winter) and combined with telemetry data (summer combined and winter combined). Parameters include: predictor variables[a], g0 = baseline detection, sigma = scale parameter. Additionally, P= Parameters; logLik = strength of evidence of each model; AIC_c = AIC with small sample bias adjustment, ΔAIC_c = difference between AIC_c model and the best model; AIC_{cwt} = weight attributed to each model.

	Model (detection function= half normal)	P	logLik	AIC	AIC_c	ΔAIC_c	AIC_{cwt}
Summer							
bk	g0~bk sigma~1	3	-231	469	472.021	0	0.75
Bk	g0~Bk sigma~1	3	-233	472	475.294	3.273	0.15
sex	g0~1 sigma~1	2	-236	476	477.411	5.39	0.05
0	g0~b sigma~1	3	-235	476	479.468	7.447	0.02
h	g0~Sex sigma~1	3	-236	478	480.944	8.923	0.01
b	g0~h2 sigma~1 pmix~h2	4	-236	480	486.578	14.56	0
Winter							
bk	g0~bk sigma~1	3	-152	309	313.204	0	0.85
Bk	g0~Bk sigma~1	3	-154	313	317.222	4.018	0.11
sex	g0~1 sigma~1	2	-157	318	319.777	6.573	0.03
0	g0~b sigma~1	3	-157	320	323.915	10.71	0
h	g0~Sex sigma~1	3	-157	320	324.059	10.86	0
b	g0~h2 sigma~1pmix~h2	4	-157	322	330.063	16.86	0
Summer combined							
bk	lambda0~bk sigma~1 hazard	3	-541	1089	1092.21	0	1
Bk	lambda0~Bk sigma~1 hazard	3	-549	1104	1107.3	15.09	0
sex	lambda0~1 sigma~1 hazard	2	-553	1111	1112.09	19.88	0
0	lambda0~b sigma~1 hazard	3	-551	1109	1112.12	19.91	0
h	lambda0~Sex sigma~1 hazard	3	-552	1110	1113.12	20.91	0
b	lambda0~h2 sigma~1 pmix~h2 hazard	4	-550	1109	1115.41	23.2	0
Winter combined							
bk	lambda0~bk sigma~1 hazard	3	-230	465	469.184	0	0.43
Bk	lambda0~Bk sigma~1 hazard	3	-230	466	470.104	0.92	0.27
sex	lambda0~1 sigma~1hazard	2	-233	470	471.285	2.101	0.15
0	lambda0~bsigma~1hazard	3	-233	472	475.569	6.385	0.02
h	lambda0~Sexsigma~1hazard	3	-232	470	473.934	4.75	0.04
b	lambda0~h2 sigma~1pmix~h2hazard	4	-228	464	472.325	3.141	0.09

[a] Predictor variables used in the construction of density models in "secr" package (Efford 2018): bk=Animal x site learned response; Bk= Animal x site transient response; sex= Capture probabilities differ between sexes; 0= Capture probabilities are homogeneous among individuals; h= Individual heterogeneity; and b= Learned response.

Supplementary material S3. Estimation of habitat available for each individual using Minimum Convex Polygon 100% (MCP) from Tirelli et al. (2018).

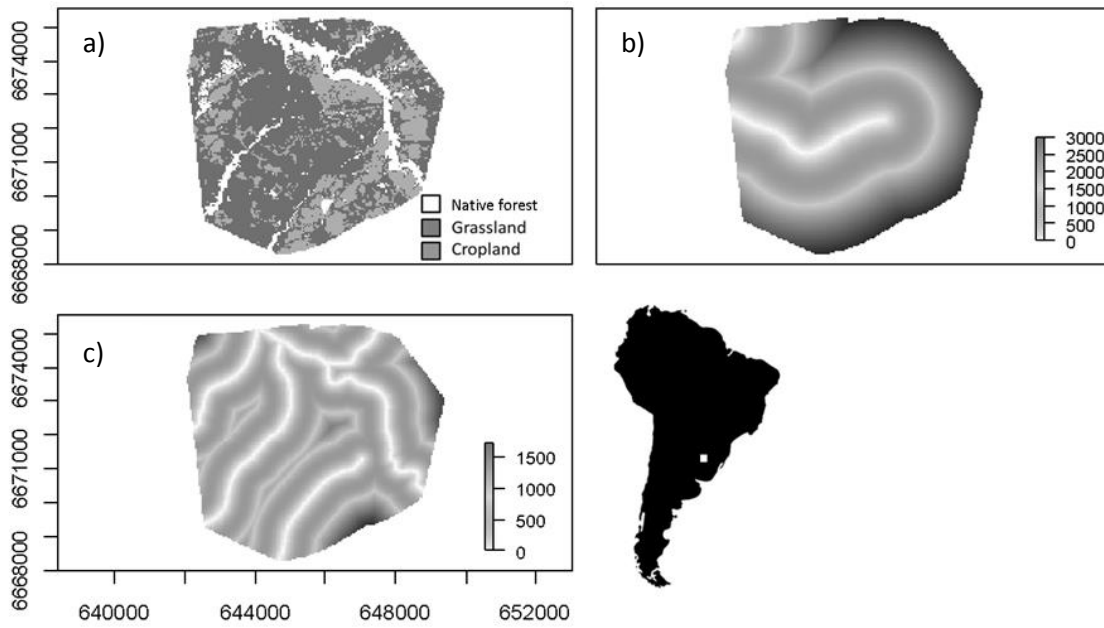| Individual	N relocations	100% MCP (km²)
M1	59	2.46
M2	54	1.87
M3	23	0.86.
M4	62	6.18
F1	34	0.75
F2	133	1.87
F3	69	0.63

Supplementary material S4. General Linear Models ('lme4' package (Bates et al., 2015) in R) and their corresponding AIC values. BIC= *Bayesian information criterion*; logLik = strength of evidence for each model; deviance=measure of goodness of fit; df.resid =residual degrees-of-freedom.

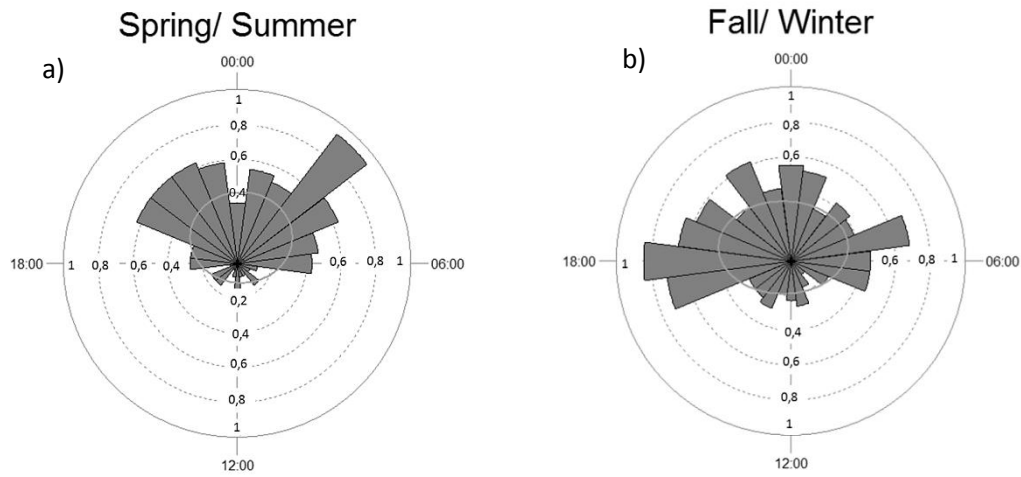| Models	AIC	BIC	logLik	deviance	df.resid
use ~ relevel(veg,"CR")+ d_road + d_river+(1|id)	2573.0	2610.7	-1280.5	2561.0	3928
use ~ d_river+(1|id)	2591.3	2610.1	-1292.6	2585.3	3931
use ~ veg + d_road+(1|id)	2592.8	2624.2	-1291.4	2582.8	3929
use ~ d_road +(1|id)	2614.9	2633.7	-1304.4	2608.9	3931
use ~ relevel(veg,"RV")+(1|id)	2625.4	2650.5	-1308.7	2617.4	3930
use ~ relevel(veg,"GR")+(1|id)	2625.4	2650.5	-1308.7	2617.4	3930
use ~ relevel(veg,"CR")+(1|id)	2625.4	2650.5	-1308.7	2617.4	3930
use ~ veg+(1|id)	2625.4	2650.5	-1308.7	2617.4	3930
use ~ 1|id	2663.0	2675.5	-1329.5	2659.0	3932

Supplementary material S5. Mean (hours:minutes) and standard deviation (minutes) for time of sunrise, time of sunset and duration of daylight collected during the entire study period of study and divided between two seasons; data obtained for the Alegrete municipality (which includes most of our study site), RS, Brazil.

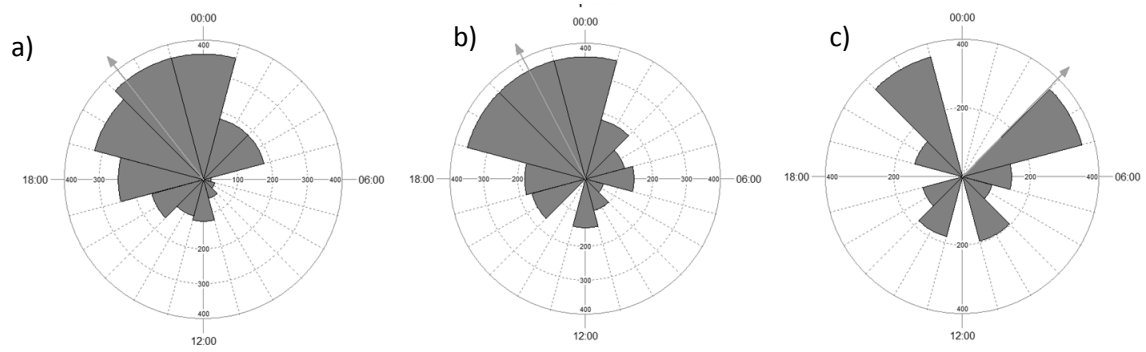|	Sunrise		Sunset		Duration of daylight	
	Mean	SD	Mean	SD	Mean	SD
All seasons	07:02	0.98	19:04	2.72	12:01	3.35
Summer-spring	06:57	0.69	20:03	1.83	13:16	3.25
Fall-winter	07:15	0.84	18:10	0.69	10:54	1.50

*Data base collected from © 2011-2016 sunrise-and-sunset.com

Supplementary material S6. Variables used in Resource Selection Function analyses performed in this study. a) Habitat composition (with three categories: native forest, grassland and cropland). b) Distance to road (meters). c) Distance to water (meters). Coordinate system UTM Zone 21J.

Supplementary material S7. Seasonal activity patterns of Geoffroy's cats in the Brazilian pampas in two different seasons. Bars indicate the proportion of camera-trap records taken at that hour of the day. Grey line is the Standard deviation ellipse. a) Spring-summer (n=240). b) Fall-winter (n=273).

Supplementary material S8. Circadian activity patterns of Geoffroy's cats in the Brazilian pampas in three different habitats: a) native forest, b) croplands, and c) grasslands. Bars indicate the proportion of active records with respect to the total number of fixes at that hour of the day. Arrows represent the mean time of activity.