Biologging as an important tool to uncover behaviors of cryptic species (#75326)

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Biologging as an important tool to uncover behaviors of cryptic species

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Advances in biologging have increased the understanding of how animals interact with their environment, especially for cryptic species. For example, giant armadillos (*Priodontes maximus*) are the largest extant species of armadillo but are rarely encountered due to their fossorial and nocturnal behavior. Through the analysis of speed, turning angles, and accelerometer activity counts, we estimated behavioral states, characterized activity budgets, and investigated the state-habitat associations exhibited by individuals monitored with GPS telemetry in the Brazilian Pantanal from 2019 to 2020. This methodology is proposed as a useful framework for the identification of priority habitat. Using a non-parametric Bayesian mixture model, we estimated four latent behavioral states that were named 'vigilance-excavation', 'local search', 'exploratory', and 'transit'. These states appeared to correspond with behavior near burrows or termite mounds, foraging, ranging, and rapid movements, respectively. The first and last hours of activity presented relatively high proportions of the vigilance-excavation state, while most of the activity period was dominated by local search and exploratory states. The vigilance-excavation state occurred more frequently in regions between forest and closed savannas, whereas local search was more likely in high proportions of closed savanna. Exploratory behavior probability increased in high proportions of both forest and closed savanna. Our results establish a baseline for behavioral complexity, activity budgets, and habitat associations in a pristine environment for future work that investigates anthropogenic impacts on giant armadillo behavior and fitness. The integration of accelerometer and GPS-derived movement data through our mixture model has the potential to become a powerful methodological approach for the conservation of other cryptic species.

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22

23 **Abstract**

24 Advances in biologging have increased the understanding of how animals interact with their

25 environment, especially for cryptic species. For example, giant armadillos (*Priodontes maximus*)

26 are the largest extant species of armadillo but are rarely encountered due to their fossorial and

27 nocturnal behavior. Through the analysis of speed, turning angles, and accelerometer activity

28 counts, we estimated behavioral states, characterized activity budgets, and investigated the state-

29 habitat associations exhibited by individuals monitored with GPS telemetry in the Brazilian

30 Pantanal from 2019 to 2020. This methodology is proposed as a useful framework for the

31 identification of priority habitat. Using a non-parametric Bayesian mixture model, we estimated

32 four latent behavioral states that were named 'vigilance-excavation', 'local search',

33 'exploratory', and 'transit'. These states appeared to correspond with behavior near burrows or

34 termite mounds, foraging, ranging, and rapid movements, respectively. The first and last hours of

35 activity presented relatively high proportions of the vigilance-excavation state, while most of the

36 activity period was dominated by local search and exploratory states. The vigilance-excavation

37 state occurred more frequently in regions between forest and closed savannas, whereas local

38 search was more likely in high proportions of closed savanna. Exploratory behavior probability

39 increased in high proportions of both forest and closed savanna. Our results establish a baseline

40 for behavioral complexity, activity budgets, and habitat associations in a pristine environment for

41 future work that investigates anthropogenic impacts on giant armadillo behavior and fitness. The

42 integration of accelerometer and GPS-derived movement data through our mixture model has the

43 potential to become a powerful methodological approach for the conservation of other cryptic

44 species.

45

46   Keywords: accelerometry, Bayesian mixture model, habitat requirements, Neotropical savannas,

47   *Priodontes maximus,* telemetry

Introduction

48

49   Movement ecology provides increasingly detailed information on spatiotemporal

50   movement patterns of species, contributing to the understanding of how animals navigate

51   through different landscapes (Fraser et al. 2018). In particular, understanding animal behavior in

52   preferred habitats, especially in pristine environments, can help inform effective habitat

53   conservation measures and even policy decisions (Fraser et al. 2018). Given that animal

54   movement patterns are affected by human activities that alter natural habitats (Tucker et al.

55   2018), behavioral changes from baseline activity levels in pristine environments may provide a

56   proxy for the effect of disturbance.

57   Animal trajectories can be decomposed into two basic components, step lengths and

58   turning angles. Step lengths are characterized by the distance between consecutive animal

59   locations and turning angles are the angular deviation between headings of consecutive steps

60   (Turchin 1991). These components help to characterize the velocity and the tortuosity along a

61   movement path, which are related to the activities performed over time. Additionally, biologging

62   devices that record fine-scale movement patterns (e.g., accelerometers) can provide new insight

63   on the spatial ecology and behavior of species. Together, data from these movement metrics

64   enable the reconstruction of trajectories and the identification of short-term latent (or

65   unobserved) behavioral states that influence the fitness and distribution of individuals (Fryxell et

66   al. 2008; Morelle et al. 2017). An individual's behavioral state can change in response to internal

67   and external stimuli experienced along its path (Nathan et al. 2008). Hence, exhibited behaviors

68   may be linked not only to the species' life history traits, but also to factors such as habitat use,

69   foraging, predation risk and social behavior (Forester et al. 2007; Gurarie et al. 2011).

70   The giant armadillo *Priodontes maximus* Kerr, 1792 (Mammalia: Cingulata), the largest

71   extant armadillo species, is a cryptic fossorial mammal native to South America. This species

72   spends 80% of its time resting underground, only emerging from its deep burrows at night to

73   feed on termites and ants (Desbiez et al. 2021). Giant armadillos select mainly forests and closed

74   savannas to perform their aboveground activities (Desbiez et al. 2020a). In addition, these

75   solitary mammals occur at naturally low densities (Desbiez et al. 2020b). The combination of

76   these characteristics makes the study of giant armadillos notoriously difficult in the wild (Carter

77   et al. 2016). Importantly, this species is currently classified as "Vulnerable" (A2cd) on the IUCN

78   Red List of Threatened Species due to habitat loss, hunting, and illegal animal trafficking

79   (Anacleto et al. 2014).

80   When directly observed, giant armadillos are most frequently performing either

81   directional displacement, vigilance behavior while standing on their hind feet, moving relatively

82   slowly using their sense of smell to assess the environment, digging termite mounds and portions

83   of soil for feeding, or digging burrows for sheltering. Nevertheless, direct observations are rare

84   and most knowledge on their behavior comes from camera trap records and inferences based on

85   telemetry methods (Desbiez et al. 2020c,d). These studies have revealed that selection of

86   landscape features varies over ontogeny, between males and females, and even according to

87   activity status (activity vs rest; Desbiez et al. 2020a). However, do not know how giant

88   armadillos use the landscape to perform different aboveground behaviors, the diversity of their

89   behavioral repertoire, nor the relative time allocated to each behavior.

90   According to optimal foraging theory (Calow and Townsend 1981), animal behavior

91   (including behavioral repertoire and associated activity budgets) is constrained by both energy

92   expenditure and gain per behavior. Each behavior contributes differently to individual fitness and

93   may be optimized in particular habitat features. Hence, discerning the behavioral processes that

94   underlie animal movement patterns and their habitat associations may be used to investigate the

95   effect of anthropogenic habitat degradation on individual fitness (Pagano et al. 2020; Picardi et

96   al. 2022). In addition, the behavioral complexity and activity budget of giant armadillos are of

97   special interest, given that this species has one of the lowest basal metabolic rates among

98   placental mammals (McNab 1985), which may lead to energetically constrained activity patterns

99   and behavioral repertoire (Ancona and Loughry 2009).

100   While there has been an increased effort to understand the movement and spatial ecology

101   of giant armadillos within the Brazilian Pantanal (Desbiez et al. 2020a,c), quantitative measures

102   of latent behavioral states and their relationships with environmental covariates have not yet

103   been evaluated. The estimation of latent behavioral states from animal telemetry data can

104   elucidate which behaviors are exhibited over time and their correspondence with resources

105   across the landscape. To better understand behavioral patterns of giant armadillos over space and

106   time, our objectives were to 1) estimate latent behavioral states from high-resolution

107   biotelemetry data, 2) characterize daily activity budgets, and 3) investigate the association

108   between behavioral states and habitat types based on a combination of GPS and accelerometer

109   data.

110

111   **Materials & Methods**

112   *Study area*

113   The study region consists of a 350 km^2 area of the Brazilian Pantanal, one of the world's

114   largest floodplains, which has a semi-humid tropical (Aw) climate (Soriano 2000). The

115   landscape is a natural mosaic of different habitats, including semi-deciduous forests, closed

116   savanna, open savanna, permanent and seasonal ponds, as well as natural and exotic grasslands.

117   The Pantanal experiences dry (April – September) and wet seasons (October – March), which

118   impacts the distribution of surface water across the landscape (Soriano 2000, Harris et al. 2005).

119   Traditional cattle ranching is practiced within the study area, although its impact is considered to

120   be minimal because of the low density of cattle and low landscape conversion rates (Harris et al.

121   2005). Compared to other regions in Brazil (and the rest of South America) that are occupied by

122   giant armadillos, this study area is considered to be relatively pristine (Venter et al. 2016).

123   Therefore, the behavioral states and activity budget characterized by this study may provide

124   baseline data for giant armadillos in a landscape that has low anthropogenic impact.

125

126   *Capture and tagging*

127   Seven giant armadillos were captured and anesthetized following methods described in

128   Desbiez et al. (2020c) from May to October 2019 (Fig. 1). Once sedated, armadillos were fitted

129   with a VHF radio transmitter (IMP 310, Telonics, Inc., Mesa, AZ) and an external archival

130   biologging device (TGW-4100-2, Telonics, Inc., Mesa, AZ) that included both GPS and

131   accelerometer. The VHF transmitter weighed 38.5 g (~1.3% armadillo body mass) and was

132   implanted intra-abdominally following surgical procedures in Kluyber et al. (2020), whereas the

133   biologging device weighed 71 g (~2.37% armadillo body mass) and was externally attached to

134   the animal's carapace following methods in Silveira et al. (2009). After procedures were

135   finished, anesthesia was reversed and armadillos were allowed to fully recover before release

136   (Desbiez et al. 2020c, Kluyber et al. 2020). Biologging devices were retrieved for archival data

137   download once they fell off the armadillos. Five individuals, biologging devices were re-

138   deployed a second time after locating the armadillo via VHF telemetry. All animal handling was

139   performed following the Guidelines of the American Society of Mammalogists (Sikes et al.

140   2016) and under License No. 27587 from the Chico Mendes Institute for Biodiversity

141   Conservation, which granted permission to capture, immobilize, and manipulate armadillos.

142   For each deployment of biologging devices, GPS fixes were programmed to record every

143   7 min while the accelerometer was programmed to record every 5 min. The tri-axial

144   accelerometer of the biologging device was programmed to summarize measurements into an

145   "activity count" variable per time interval. This variable was calculated by detecting any values

146   of acceleration greater than zero across each of the three axes per second of the time interval.

147   This means that the magnitude of acceleration is not the focus of activity counts, but rather the

148   overall frequency of movements. For example, an individual that is walking for every second of

149   a 5 min interval (300 s) would have an activity count of 300, which would be equivalent to the

150   same individual sprinting for the same duration. It should be noted that the accelerometer does

151   not rely on satellite coverage and provides measurements independent of the GPS fixes.

152

153   *Data preparation*

154   We recorded in total 18,433 GPS fixes and 140,162 accelerometer measurements from all

155   seven monitored individuals. To remove error-prone measurements that could bias the analysis

156   and results, the dataset was filtered. First, we removed aberrant locations due to low satellite

157   coverage (≤ 4 satellites) and, because ==goal was to understand active behavior outside the==

158   ==burrow==, we also removed activity counts recorded as zero. Then, we calculated step lengths

159   between successive GPS locations for each individual and excluded step lengths that were larger

160   than biologically possible for the time interval (> 800 m in 7 min; 99th quantile). Because giant

161   armadillos rest in deep burrows during the day, ==re GPS fixes cannot be acquired, only active==

162 <mark>movements above ground with associated GPS fixes were evaluated</mark>. Moreover, GPS positions

163 were filtered to only include observations successfully sampled at 7 ± 1 min time intervals. Since

164 activity counts were recorded at a different time interval than GPS locations (5 vs 7 min,

165 respectively), only activity counts recorded within 1 min of GPS positions were retained to

166 maintain comparable measurements. Step lengths were converted to speed by dividing its value

167 by the time interval between consecutive locations (e.g., 7 min). After completing these filtering

168 steps, a total of 9,948 observations of both location and activity count were retained for further

169 analysis (Table 1; Fig. 1).

170

171 *Latent behavioral state estimation*

172   We relied on activity count, speed (as calculated above), and turning angle for the

173 estimation of latent behavioral states using a non-parametric Bayesian mixture model (Valle et

174 al. 2022). Each variable was discretized into bins as required by the model, where the number

175 and width of bins were selected to characterize the continuous distributions in as few bins as

176 necessary (Cullen et al. 2022). Activity count ranged from 1 to 300 and was discretized into 6

177 bins of equal width. Speed ranged from 0 to 2.13 m/s and was discretized into 7 bins. Since 99%

178 of speed observations were recorded below 1 m/s, 6 bins of equal width were used to discretize

179 speed from 0 to 1 m/s. All observations greater than 1 m/s (up to 2.13 m/s) were assigned to the

180 7th bin. <mark>Turning angle ranged from $-\pi$ to π radians</mark> and was discretized into 10 bins of equal

181 width. <mark>Given that GPS locations were not available while armadillos rested in their burrows, this</mark>

182 <mark>analysis estimated only active states</mark>.

183   The three discretized variables (i.e., activity count, speed, and turning angle) were

184 analyzed using a non-parametric Bayesian mixture model using the package `bayesmove` v0.2.0

185   (Cullen et al. 2022) in the R statistical software (v4.0.2; R Core Team 2020). This model clusters

186   observations (pooled across all individual tracks) into an unknown number of discrete latent

187   behavioral states. Using a penalizing Bayesian prior, we only need to specify the maximum

188   number of possible behavioral states and the model estimates the most likely number of states

189   assigning these to observations. The model was run using 20,000 Markov chain Monte Carlo

190   (MCMC) iterations where the first 10,000 iterations were treated as the burn-in, the maximum

191   number of possible states was set to 10, and the hyperparameter α was set to 0.1. Convergence to

192   the posterior distribution was assessed by evaluating the log likelihood trace plot. This model

193   took 18 min to run on a 2.6 GHz i7 CPU with 16 GB RAM.

194   The number of latent states was determined by assessing the probability of state

195   assignments as well as the biological relevance of the state-dependent distributions. Specifically,

196   the most likely number of states was estimated by calculating the average probability that

197   observations belonged to a particular state and selecting the set of states that together represented

198   ≥90% of all observations. Additionally, following Pohle et al. (2017) recommendations, state-

199   dependent distributions of activity counts, speed and turning angles were inspected so that only

200   biologically interpretable states were retained. To ensure high certainty of behavioral state

201   assignments, ≥ 75% of all posterior estimates of a given observation needed to belong to a single

202   state. If none of the states for a given observation fell above this threshold, the observation was

203   labeled as 'unclassified'.

204

205   *Activity budgets*

206   To determine diel patterns of behavior, activity budgets were calculated with all

207   individuals pooled together. Hourly counts of biologging transmissions were calculated, as well

208   as the relative proportion of behavioral states exhibited for each hour. Unclassified observations

209   were omitted from the quantification of activity budgets to emphasize the relationships among

210   classified states. Diel activity patterns were qualitatively examined to determine when giant

211   armadillos were most active and to explore temporal patterns in the estimated behavioral states.

212

213   *Behavioral state-habitat associations*

214   To understand the relationship between the estimated behavioral states and the habitat

215   used by giant armadillos within the study area, we extracted land use/land cover (LU/LC) classes

216   at each location of each individual. The LU/LC data was obtained via supervised classification of

217   Landsat 8 imagery from 2018 as described in Desbiez et al. (2020a). Four classes of LU/LC were

218   identified separately for the dry (April - September) and wet (October - March) seasons: forest,

219   closed savanna, open savanna, and floodable grasslands (Fig. 2). Floodable grasslands are

220   completely or partially flooded during the flood season and covered by grassland and sparse

221   shrubs during the dry season. LU/LC was extracted using a 30 m buffer around each GPS

222   position using the R package `raster` v3.4-10 (Hijmans 2021). This buffer was adopted to

223   capture local habitat heterogeneity for a given location and to account for GPS location error.

224   Since LU/LC is a discrete variable, the proportion of each class within the buffer was calculated

225   for all observations.

226   To assess the behavioral state-habitat associations across the local landscape, we fitted a

227   Bayesian multinomial logistic regression to evaluate how the prevalence of each state was

228   influenced by LU/LC (Wilkinson et al. 2019). This model estimated the probability of exhibiting

229   each of the behavioral states with respect to the state (i.e., the reference state). Fixed effects

230   were included for the proportion of the forest, open savanna, and floodable grassland classes,

231   whereas closed savanna was chosen as the baseline LU/LC class and therefore was omitted from

232   the list of covariates. Quadratic terms were included for each LU/LC class to account for non-

233   linear relationships. Armadillo ID was treated as a random effect on the intercept to account for

234   individual heterogeneity. To fit this model, we used the R package `brms` v2.16.3 (Bürkner 2017)

235   with a categorical distribution and logit link function, where the no-U-turn sampler (NUTS;

236   Hoffman and Gelman 2014) from Hamiltonian Monte Carlo was used via Stan (Stan

237   Development Team 2020) to obtain posterior distribution samples. Regularized priors were used

238   for model parameters to keep estimates within the plausible domain space, which was verified by

239   a prior predictive check (Wesner and Pomeranz 2021). We ran 4 chains with a warmup of 1000

240   iterations and retained 1000 iterations from the posterior distribution, resulting in a total of 4000

241   samples from the posterior. Model convergence was assessed by inspecting trace plots, effective

242   sample size, and $\hat{R}$ (Vehtari et al. 2021) for each parameter, while model fit was assessed through

243   a posterior predictive check (Gabry et al. 2019; Gelman et al. 2020). After running the model,

244   trace plots appeared to exhibit stationarity, the effective sample size was near the total number of

245   posterior samples, and $\hat{R}$ was equal to 1.00 for all estimated parameters, indicating model

246   convergence.

247

248   **Results**

249   *Latent behavioral state estimation*

250   The mixture model suggested that four states were likely present for these data

251   (accounting for 98% of all observations) based on the aforementioned threshold and inspection

252   of the state-dependent distributions. These states were labeled as 'vigilance-excavation' (VE),

253   'local search', 'exploratory', and 'transit' (Fig. 3). The VE state is characterized by relatively

254   low activity counts, low speed, and high turning angles (near $-\pi$ or π radians), which is

255   congruent with the movements observed when armadillos are exhibiting vigilant behavior or

256   when excavating either termite mounds or new burrows. The local search state is nearly identical

257   to the VE state for distributions of activity counts and speed, but has a more uniform distribution

258   of turning angles that is expected to occur when armadillos are performing an area-restricted

259   search for food. The exploratory state is characterized by higher activity counts, greater speed,

260   and lower turning angles (near 0 radians) than either the VE or local search states, which reflects

261   a relatively faster and more directed movement that can be associated with ranging movements,

262   most likely to find food. Lastly, the transit state exhibited the greatest activity counts, greatest

263   speeds, and lowest turning angles, reflecting fast and directed movements with the primary

264   purpose of displacement between two areas, as movement speed and high directionality would

265   unlikely allow foraging or other activities during this behavioral state. Of the 9,948 observations

266   analyzed by this model, 38% were labeled as 'unclassified' since the state assignments from the

267   posterior distribution did not overwhelmingly belong to a single state. The remaining 6,180

268   observations were classified as one of the four estimated behavioral states.

269

270   *Activity budgets*

271   Giant armadillos were most active during the middle of the night and displayed notable

272   differences in the temporal patterns exhibited by each behavioral state. The greatest number of

273   joint GPS and accelerometer measurements from the biologging device (>600 measurements per

274   hour) occurred between 20:00 and 01:00 across all tagged individuals (Fig. 4). However, it

275   appears that armadillos can be active at any time throughout the course of the night, including

276   dusk and dawn. On average, armadillos dedicated most of their active time to local search (44%)

277   and exploratory states (33%), whereas VE (19%) and transit states (4%) were observed less

278   frequently. When evaluated on an hourly basis, the local search and exploratory states showed

279   minimal changes in their frequency throughout the night (Fig. 4b). By comparison, the VE state

280   was exhibited in greatest proportions at the very first and last hours of recorded activity, whereas

281   the transit state was exhibited in greatest proportion during the second to last hour of activity

282   (Fig. 4b).

283

284   *Behavioral state-habitat associations*

285   Strong relationships were found between specific land cover classes and behavioral

286   states. The likelihood of displaying the VE state increased when armadillos were in areas with

287   high proportions of open savanna and floodable grasslands (>80% cover) or areas of transition

288   between forest and closed savannas (Fig. 5, Table S1). The probability of performing the

289   exploratory state increased in areas with high proportion of forest cover and low proportion of

290   closed savanna, and in areas with low proportion of forest cover and high proportion of closed

291   savanna, with lower probability in areas with intermediate coverage of both LU/LC classes.

292   Additionally, armadillos displayed a low overall probability of being in a transit state and no

293   significant trends were detected. Finally, although local search behavior was the most likely state

294   to be exhibited across each of the evaluated LU/LC classes, a negative relationship was found

295   with increasing proportions of forest, open savanna, and floodable grasslands (Fig. 5, Table S1).

296   These results imply that local search was more likely in areas with high proportions of closed

297   savanna. Posterior distributions for each of the parameter estimates from the multinomial

298   regression are shown in Fig. S1 and the probabilities of exhibiting each state when in 100% of

299   each LU/LC class are shown in Fig. S2.

300

Discussion

Identification of behavioral states in a cryptic species

Four behavioral states appeared most likely from the analysis of activity counts, speed, and turning angles in fine-scale movements. Each of the identified states appeared to reflect behaviors of giant armadillos previously observed in the field (pers. obs.), supporting the use of these results to interpret the behavior of this cryptic species. Our results also highlight the contribution of ancillary movement measures, such as accelerometry activity counts, for the identification of latent behavioral states. When analyzing only speed and turning angles, the non-parametric Bayesian mixture model was only able to identify three behavioral states, where 'exploratory' and 'transit' behaviors were grouped together (Fig. S3). The discrimination between 'exploratory' and 'transit' behavior is especially important in studies such as ours that to relate behavioral budgets with energetic constraints, as the former behavior is related with energy acquisition while the latter relates to direct displacement from one point to another and energy expenditure. Even though the activity counts measure from the accelerometer provides less detailed information when compared to tri-axial accelerometry, its inclusion as an additional data stream (beyond speed and turning angle) appears to have assisted in greater discrimination among behavioral states. We believe that, had our accelerometers provided more detailed information instead of a summary metric (i.e., number of seconds with activity), we would have been able reduce the proportion of unclassified records or even been able to distinguish additional behaviors. Nevertheless, more research is needed to determine if this is likely to be true.

322

323   *Activity budgets*

324   This study reveals that giant armadillos are most active during the middle of the night

325   (20:00 – 01:00; Fig. 4) Although we detected armadillo activity at varying levels throughout

326   the entire night, recorded activity only lasted approximately 5 hours on average each day,

327   corroborating the results found by Desbiez et al. (2021) using a different set of data and

328   analytical approaches in the same study region.

329   Proportions of local search and exploratory states were both high throughout the entire

330   nightly activity period and together represented 77% of all the classified observations. Based on

331   field observations, these two behaviors may be associated with foraging activities. Previous

332   studies have shown that armadillo activity budgets are mostly oriented towards energy

333   acquisition, with very limited social interactions (Sona and Loughry 2009; 2010). Indeed, the

334   only other mammals that dedicate such high proportions of their activity budgets to foraging

335   activities are the nine-banded armadillo *Dasypus novemcinctus* (77-100%), the burrowing

336   ground squirrel *Urocitellus townsendii* (65-97%)*,* and species of arboreal marsupials from the

337   genus *Petaurus* (66-85%; Ancona & Loughry 2009). Giant armadillos are large mammals (32 –

338   60 kg), with short activity periods, low basal metabolic rates and an energy restricted diet

339   composed mostly by ants, termites and other invertebrates, which are scattered across the

340   landscape (Desbiez et al. 2021; McNab 1985; Ancona & Loughry 2009). Hence, it is not

341   surprising that most of its activity budget is spent on search and acquisition of food (i.e., local

342   search and exploratory states).

343   The relatively high proportions of the VE state during the very first and last hours of the

344   activity period are likely associated with vigilance behavior upon leaving the burrow and

345   excavating new burrows at the end of the night (Fig. 4b). predation pressure on giant

346   armadillos may be associated with the relatively small proportion of time spent on vigilance

347   throughout the night, especially when away from its shelter. Hence, the consistently low levels of

348   the VE state observed throughout the night are likely reflective of termite mound excavation

349   while foraging, which requires less persistent digging but may generate similar movement

350   patterns to those observed during vigilance or the digging of burrows.

351   Individuals rely on spatial memory or cognitive maps to survive (*sensu* Gallistel 1994;

352   but see Bennett 1996). Relatively rapid and directed movement is observed when cognitive

353   mechanisms (e.g., memory) are employed to locate resources (Polansky et al. 2015). The

354   relatively higher proportion of transit behavior near dawn could be associated with individuals

355   quickly returning to burrows, a key sheltering resource for this species (Fig. 4b). Giant

356   armadillos are range residents and use the same area for many years (Desbiez et al. 2020c; 2021).

357   They are known to reuse burrows for two to three consecutive nights and sometimes also after

358   long periods (pers. obs.). Hence, this behavior could indicate that these important sheltering

359   structures might be somehow mapped by an individual within its home range.

360

361   *State-habitat associations*

362   We found associations between certain latent behavioral states and particular habitats,

363   which provides new insight into the species movement ecology and habitat requirements. Giant

364   armadillos have been documented to excavate burrows and rest in habitats with denser forest

365   vegetation above the floodplain, while typically selecting closed savanna habitat during activity

366   (Desbiez et al. 2020a). These patterns of habitat selection are supported and explored in further

367   detail by the state-habitat relationships characterized here.

368   The likelihood of displaying the VE state increased when armadillos were in areas with

369   high proportions of open savanna and floodable grasslands. Like other species, the use of dense-

370   cover habitat by giant armadillos has been associated with reduced predation risk (Desbiez et al.

371   2020a). Hence, when reaching more open areas with higher perceived risk, animals would tend

372   to increase vigilance behavior. Nevertheless, the likelihood of presenting a VE state was also

373   higher in transition areas between forest and closed savanna, which may reflect an increase in

374   foraging-related excavation behavior in search for ground-dwelling invertebrates. The giant

375   armadillo's foraging behavior could also justify the high probability of the local search state

376   when individuals are surrounded predominantly by closed savanna. This species forages

377   preferentially in closed savanna habitats, which are always adjacent to forests in the Pantanal

378   (Desbiez et al. 2020a). Furthermore, the association of local search and VE states to closed

379   savanna and forest edges, respectively, is also corroborated by recent dietary studies based on

380   stable isotope analysis, which show that most giant armadillos feed on invertebrates from both

381   open and closed habitats (i.e., mixed C3 and C4 resources; Magioli et al. 2022). Finally,

382   exploratory behavior was most likely to be presented when individuals were surrounded by high

383   proportions of forest or closed savanna. Hence, the exploratory behavior is likely part of the

384   ch process for resources, such as food and shelter, that can be found mainly in forests and

385   closed savannas (Desbiez et al. 2020a).

386   Giant armadillos have also been shown to use floodable grasslands during the dry season,

387   which was presumed to increase their mobility due to a lack of obstacles such as dense

388   vegetation (Desbiez et al. 2020a). In our analyses, armadillos presented a low overall probability

389   of displaying the transit state and no significant relationships with LU/LC classes were detected.

390   However, there was relatively high uncertainty around these estimates, likely resulting from the

391 few observations classified as transit by the model (n=213; 3.4%). It appeared that higher speed

392 transit behavior was more likely to be exhibited in high proportions of floodable grasslands

393 compared to other habitats, corroborating the previous hypothesis that this food-poor habitat may

394 be selected to increase an individual's mobility. Nevertheless, this pattern should be further

395 explored.

396

397 *Implications for conservation planning*

398   The identification of behavioral patterns generated by the analysis of multiple individuals

399 allows us to bridge movement ecology with population processes (Morales et al. 2010) that are

400 fundamental for conservation planning. This study links latent behavioral states to occupied

401 habitat, providing critical insight on giant armadillo interactions with the surrounding landscape.

402 These findings are complementary to previous studies on resource selection in giant armadillos

403 within the Brazilian Pantanal and neighboring biomes (Desbiez et al. 2020a; Ferraz et al. 2021;

404 Magioli et al. 2022), while providing novel insights on the types and proportions of behaviors

405 exhibited in a pristine region.

406   The estimated behavioral state-habitat associations can be used to inform conservation

407 planning and decision-making as part of current conservation efforts. Our results provide

408 baseline information for how the species moves within a relatively pristine environment that

409 consists of a naturally fragmented landscape with low human pressure. Giant armadillos search

410 for resources and feed primarily in savannas and forests, while sheltering in areas of forest.

411 Furthermore, juveniles (up to 7-8.5 years old) rely almost exclusively on forest, making this

412 habitat key for population stability and growth (Desbiez et al. 2020a). Nevertheless, the

413 grassland matrix is used for transit and does not present biophysical resistance to individual

414 dispersal movement.

415   Giant armadillos tolerate some degree of habitat disturbance (Silveira et al. 2009).

416 Nevertheless, in naturally fragmented floodable savannas, each individual requires large areas

417 (25 km^2) that minimally overlap with that of conspecifics (Desbiez et al. 2020c). Future work on

418 giant armadillos tracked in regions impacted by natural and anthropogenic disturbances (e.g.,

419 agriculture, urban development, deforestation, wildfire) can then be assessed in the context of the

420 aforementioned behavioral state-habitat associations. For example, in the neighboring Cerrado

421 savanna biome, only 69 remnants of suitable habitat larger than 25 km^2 persist and are

422 surrounded by agricultural matrix (Ferraz et al. 2021). The methodological approaches adopted

423 here could be used to understand how giant armadillos can persist in fragments within a human

424 modified matrix with moderate to intense management practices. Due to its large area

425 requirements and the accelerating rate of land-use change throughout its range, giant armadillos

426 need conservation measures that go beyond the creation of protected areas (Desbiez et al. 2020a).

427 Hence, conservation efforts that increase connectivity among remnants of habitat will be key for

428 species recovery and persistence in this biome and throughout its range.

429   Changes in behavioral repertoire, activity budget, and habitat associations may help

430 conservationists to better understand the consequences of anthropogenic impacts on individual

431 behavior and fitness. For example, we would expect an increase in the probability of exhibiting a

432 vigilance state in areas of higher perceived risk (e.g., areas close to highways, with hunting

433 activities, or with domestic dogs). These perceived risks could also affect the species' activity

434 budget in areas with higher human disturbance. In addition, this multi-faceted approach could be

435 used to better understand the degree of impact from different types of anthropogenic land-use.

436   For example, state-habitat associations can be investigated to determine whether a land-use class

437   may be categorized as a resource (i.e., high probability of resource acquisition behaviors),

438   corridor (i.e., high probability of dispersal behavior), or a risk (i.e., mostly avoided by

439   individuals). Furthermore, this approach may serve as an extraordinary tool to evaluate the

440   effectiveness of conservation actions, such as the definition of ecological corridors and priority

441   areas.

442

443   **Conclusions**

444   The success of conservation measures is usually quantified through population growth

445   via survival, resource acquisition, and reproductive success (Lacy 2019). These metrics can be

446   demanding to obtain and are especially difficult to gather for cryptic, long-lived species with low

447   reproductive rates like giant armadillos. Hence, the identification of latent behavioral states, their

448   associations with landscape features, and activity budgets can provide a short-term, powerful,

449   and feasible indicator of success for conservation actions. Our results suggest that giant

450   armadillos primarily exhibit behaviors related to foraging throughout the course of their active

451   nocturnal periods, which are particularly associated with closed savanna habitat. These findings

452   provide baseline information for future investigations that explore giant armadillo movements in

453   human-impacted landscapes. We believe that the methodological approach presented here

454   provides researchers and conservationists with a useful tool to plan and evaluate management

455   actions towards the conservation of cryptic species.

456

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464

465 **Authors' Contributions**

466 Joshua Cullen, Nina Attias, Arnaud Desbiez, and Denis Valle conceived the ideas and designed

467 the methodology; Nina Attias and Arnaud Desbiez collected the data; Joshua Cullen and Denis

468 Valle analyzed the data; Joshua Cullen and Nina Attias led the writing of the manuscript. All

469 authors contributed critically to the drafts and gave final approval for publication.

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609

Figure 1

Filtered GPS trajectories from each of the seven giant armadillos (*Priodontes maximus*) monitored in the Brazilian Pantanal between 2019 and 2020 (N=9948 locations).

Each color represents an individual giant armadillo. The blue square on the inset map denotes the extent of the study area as shown by the base map with armadillo trajectories. Satellite imagery was accessed by an ArcGIS REST API.
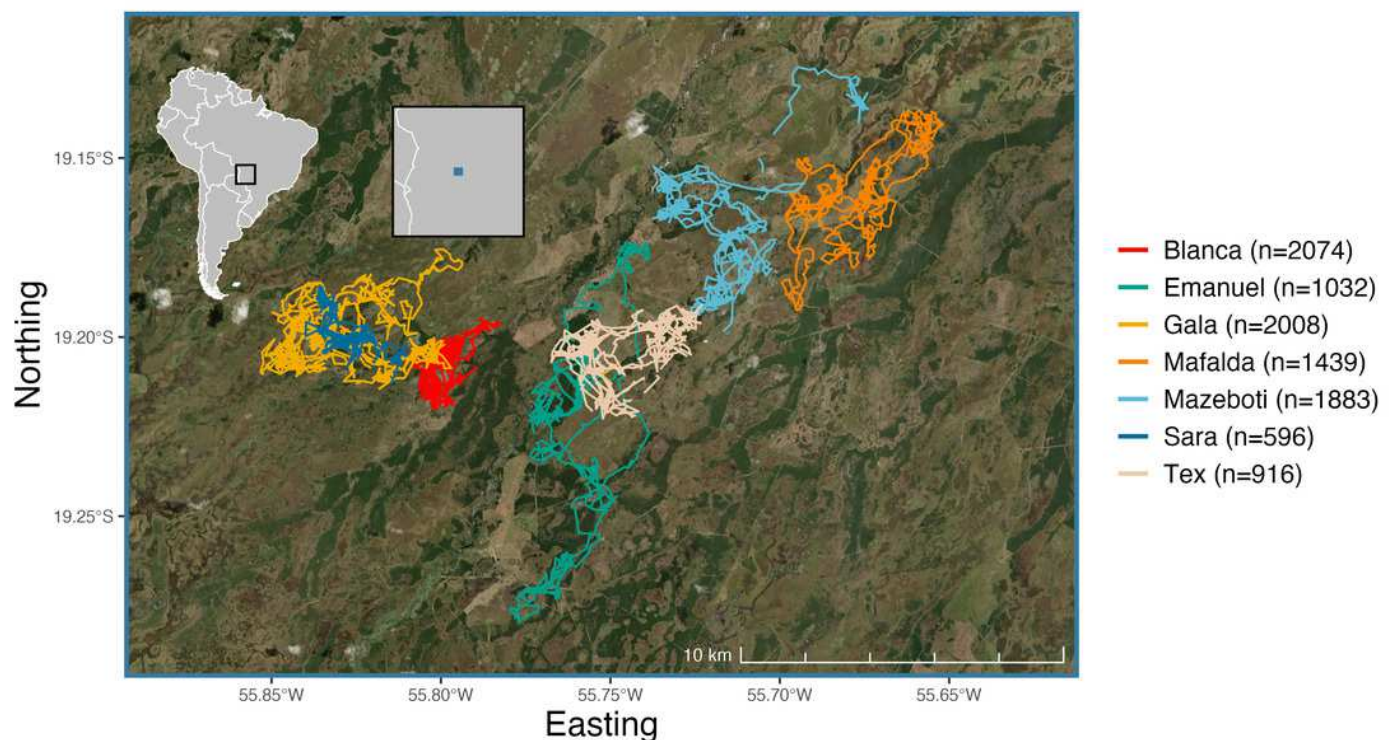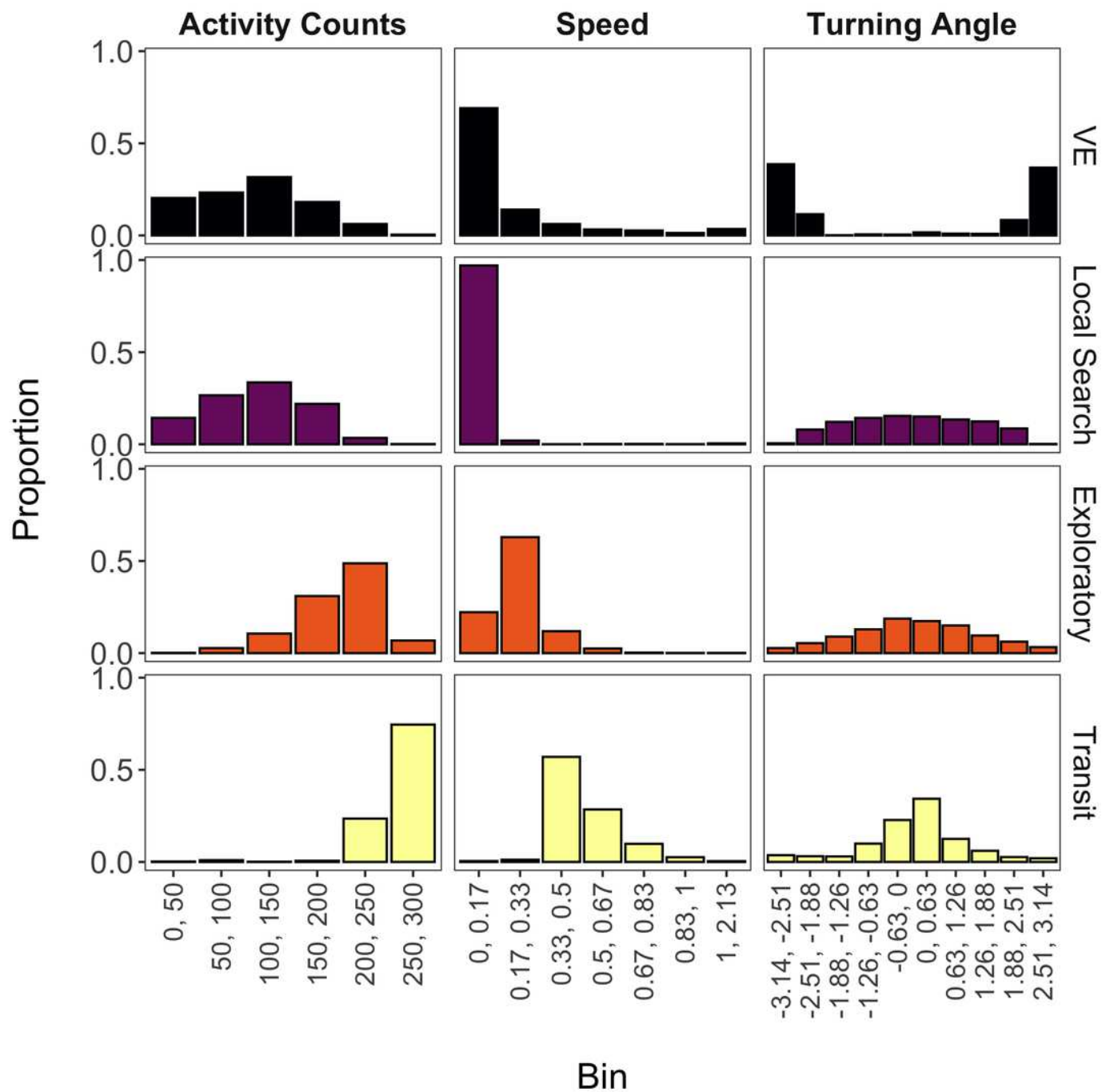
Figure 2

Landscape mosaic of land use/land cover (LU/LC) for the dry and wet seasons of the study region in the Brazilian Pantanal.
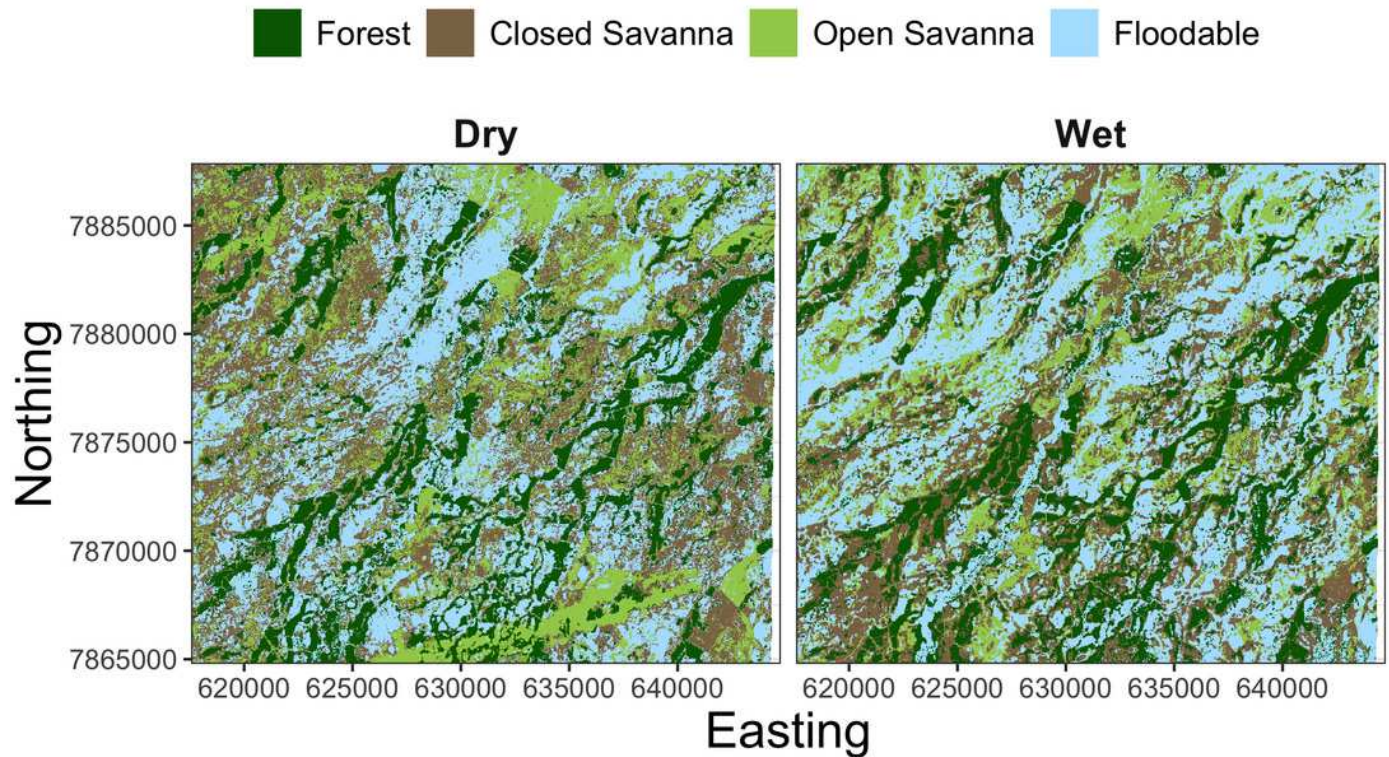
Figure 3

State-dependent distributions of activity counts, speed, and turning angle estimated by the mixture model for each of the four estimated behavioral states (vigilance-excavation [VE], local search, exploratory, and transit).

Continuous values of activity counts, speed (m/s) and turning angle (radians) were

discretized into bins. Activity counts were provided by an accelerometer, while speed and

turning angle were derived from individual GPS trajectories from seven giant armadillos

(*Priodontes maximus*) monitored in the Brazilian Pantanal between 2019 and 2020.

Figure 4

Activity budget of giant armadillos (*Priodontes maximus*; N = 7) along the diel cycle.

(a) General activity budget per hour of the day characterized by the total number of activity observations pooled across all monitored individuals. (b) Temporal patterns of behavior-specific activity characterized by the proportion of each behavioral state observed at each hour of the day. Grey shaded areas represent the maximum period from dusk to dawn (i.e., night) for the study region in the Brazilian Pantanal during the study period (2019-2020).
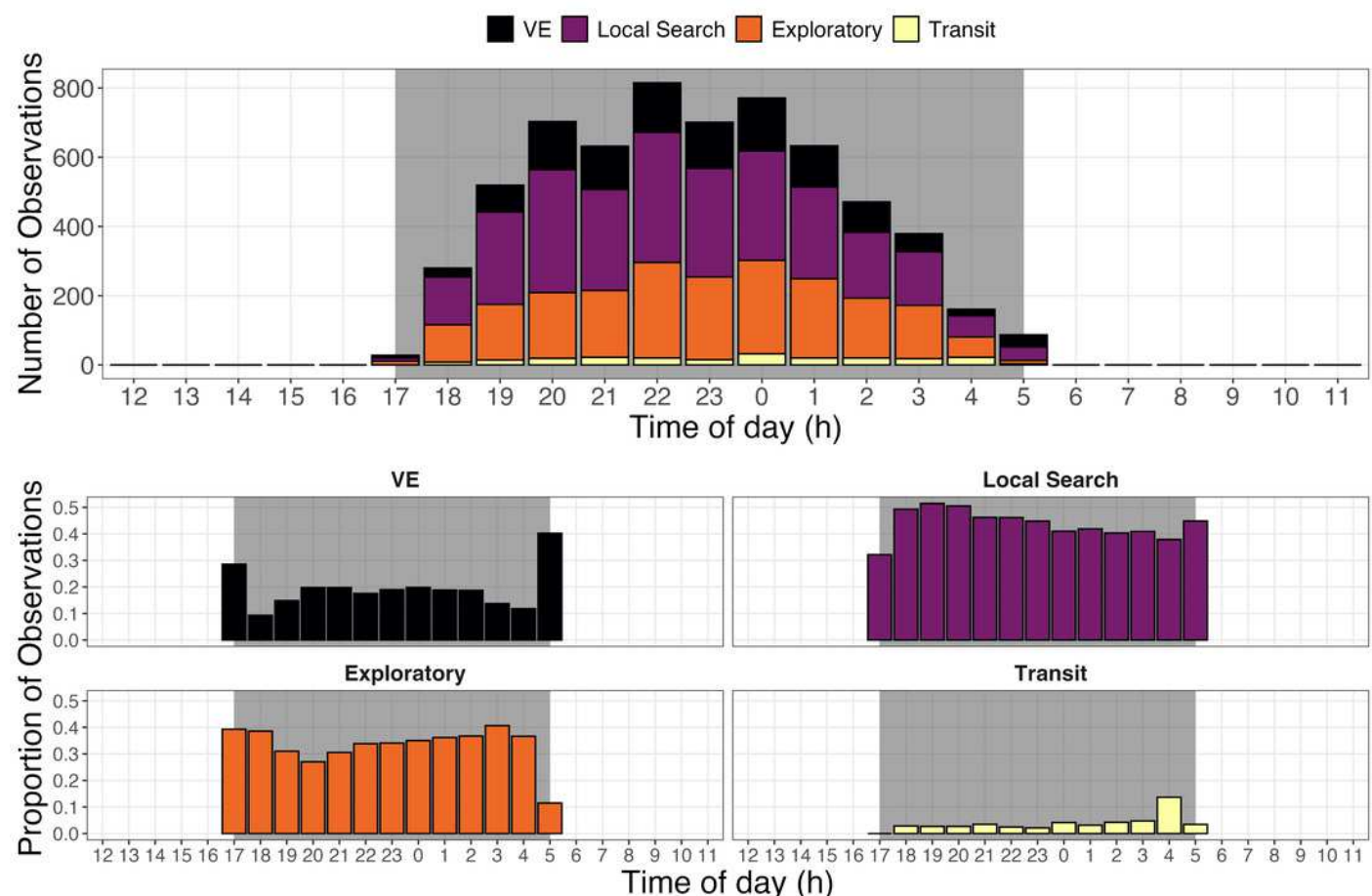
Figure 5

Probability of giant armadillos (*Priodontes maximus*) exhibiting each behavioral state as a function of the proportion of LU/LC classes in the area used.

Proportions of LU/LC classes are defined in relation to Closed Savannas (e.g., when animals are in areas with 25% of the plotted LU/LC class, the remaining 75% of the area is covered by Closed Savanna). Behavioral states are classified as: Vigilance-Excavation (VE), Local Search, Exploratory and Transit. Plot curves represent the marginal effects of the Bayesian multinomial logistic regression. Solid lines display the average response, and shaded regions denote 50% (dark) and 95% (light) credible intervals.
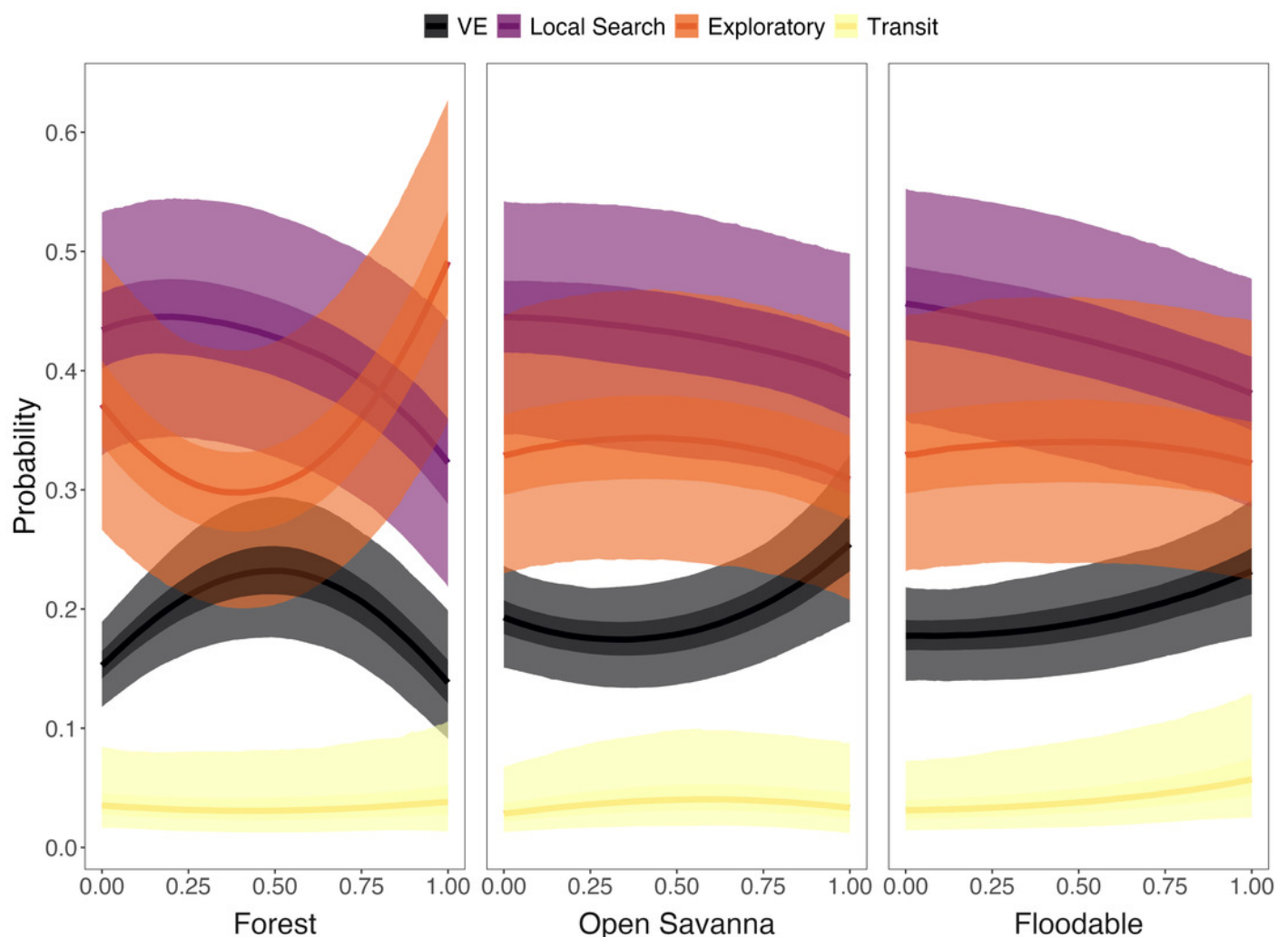
Table 1(on next page)

Summary data for the seven tagged giant armadillos (*Priodontes maximus*) from the Brazilian Pantanal (2019-2020).

Included are the ID, number of observations after data filtering (n), sex, age class, date of first tracking record, date of last tracking record, and the number of days of activity monitored.

1 Table 1. Summary data for the seven tagged giant armadillos (*Priodontes maximus*) from the

2 Brazilian Pantanal (2019-2020). Included are the ID, number of observations after data filtering

3 (sex, age class, date of first tracking record, date of last tracking record, and the number of

4 days of activity monitored.

5

ID	N	Sex	Age class	Start date	End date	Number of active days
Blanca	2074	F	Adult	2019-06-23	2019-12-04	77
Emanuel	1032	M	Adult	2019-05-19	2019-11-02	62
Gala	2008	F	Adult	2019-07-20	2019-10-29	64
Mafalda	1439	F	Subadult	2019-05-24	2019-07-13	50
Mazeboti	1883	F	Adult	2019-06-23	2020-01-24	90
Sara	596	F	Juvenile	2019-10-03	2019-11-04	32
Tex	916	F	Adult	2019-05-23	2019-12-01	63

6

SUPPLEMENTARY MATERIAL

Biologging as an important tool to uncover behaviors of cryptic species

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[f]Royal Zoological Society of Scotland (RZSS), Murrayfield, Edinburgh, United Kingdom
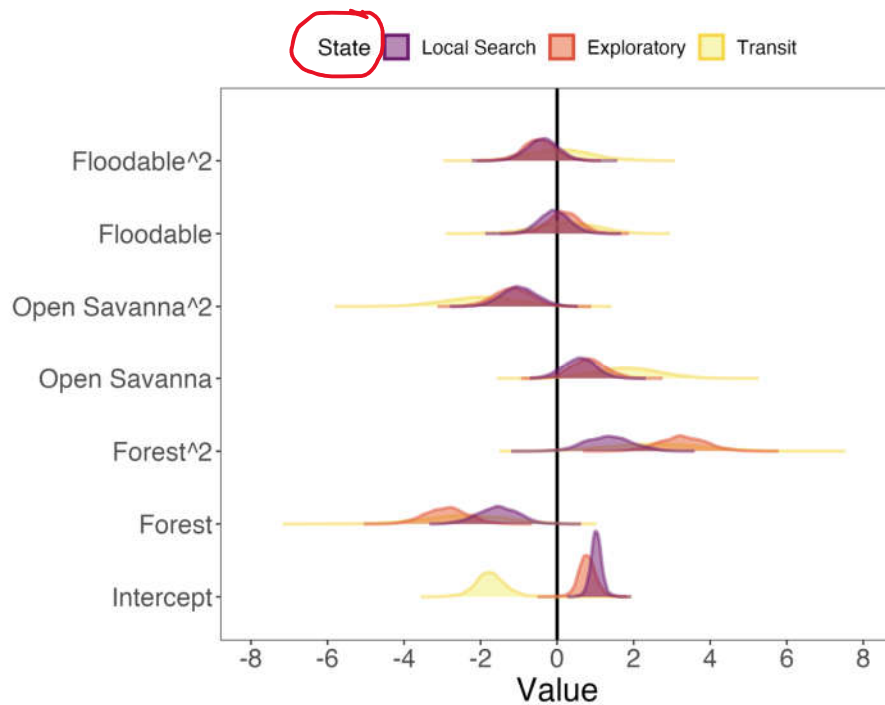
Figure S1. Posterior density distributions of parameter estimates from the multinomial logistic regression that relates proportions of land cover classes to behavioral states. The vertical line denotes a value of zero to clarify the direction and magnitude of parameter estimates.
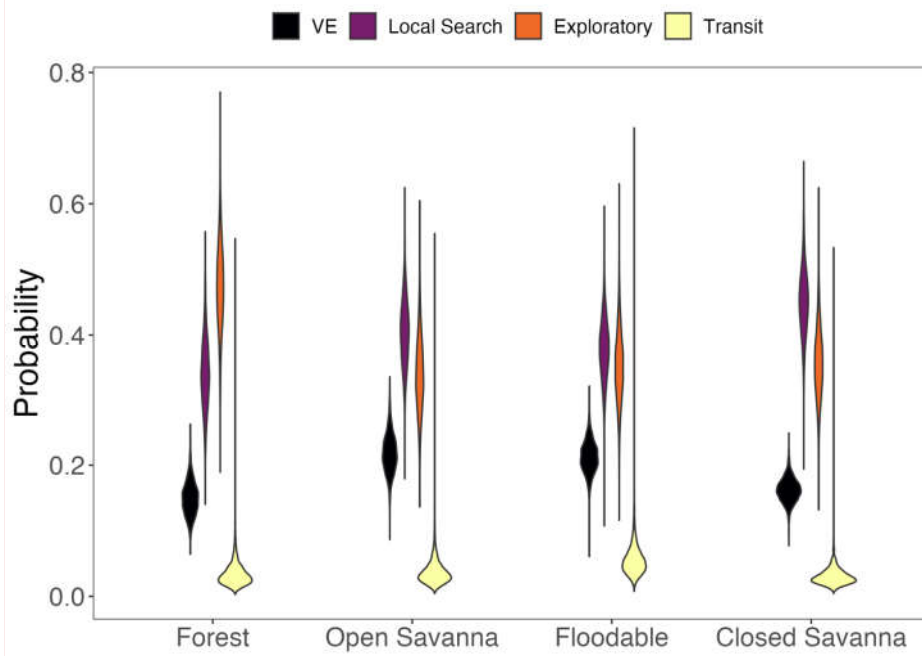
Figure S2 *Estimated probabilities of exhibiting each behavioral state when in 100% of a given land cover class as predicted by the multinomial logistic regression. The Closed Savanna class is also shown since it is the equivalent of setting all other land cover classes to 0%.*
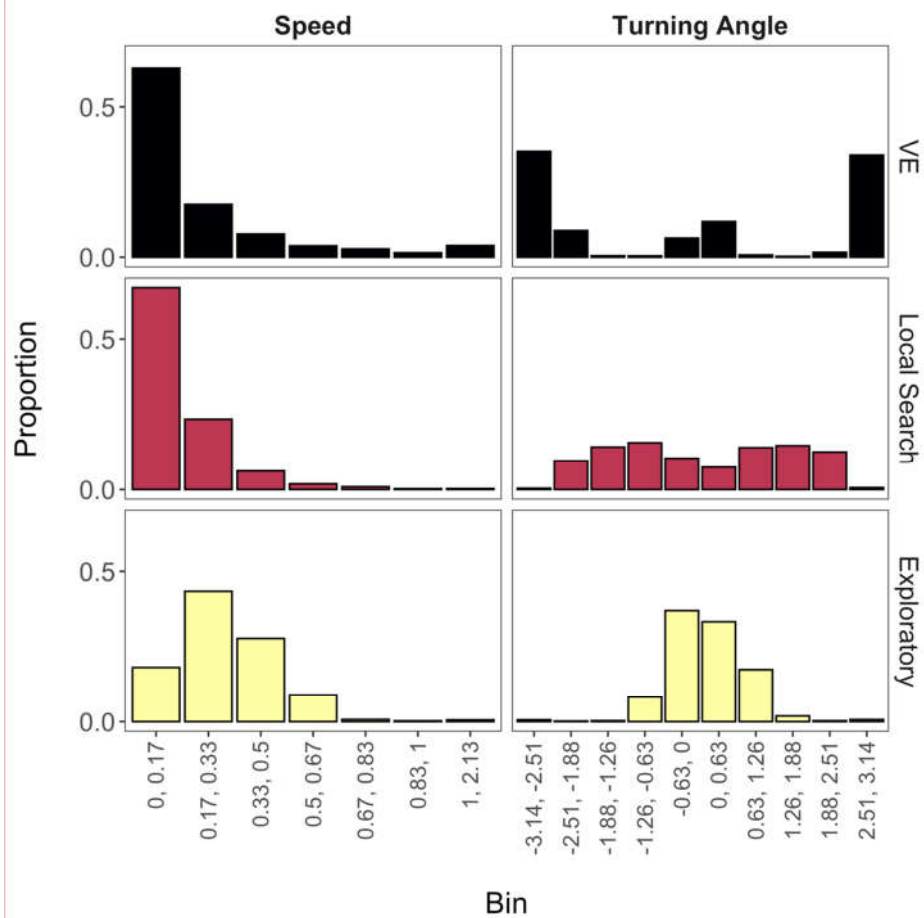
Figure S3. State-dependent distributions estimated by the mixture model for speed and turning angle are shown for each of the three identified behavioral states. The limits (min, max) associated with each bin are shown for speed (m/s) and turning angles (rad) on the x-axis.

Table S1. Model summary from the Bayesian multinomial logistic regression that relates proportion of land cover classes to each of the three estimated behavioral states. Notice that VE is the reference behavioral state and, as a result, is not included in this table. Estimates are reported on the multinomial logit scale. Bolded rows indicate the coefficients where the 95% credible interval did not contain zero.

State	Variable	Coefficient	Standard Error	95% Credible Interval
Local Search	**Intercept**	**1.02**	**0.15**	**(0.72, 1.33)**
	Forest	**-1.54**	**0.53**	**(-2.61, -0.52)**
	Forest^2	**1.34**	**0.61**	**(0.18, 2.53)**
	Open Savanna	0.58	0.42	(-0.25, 1.41)
	Open Savanna^2	**-0.99**	**0.46**	**(-1.89, -0.06)**
	Floodable	-0.06	0.40	(-0.83, 0.74)
	Floodable^2	-0.38	0.41	(-1.21, 0.41)
Exploratory	**Intercept**	**0.78**	**0.23**	**(0.33,1.23)**
	Forest	**-2.89**	**0.56**	**(-3.98, -1.79)**
	Forest^2	**3.27**	**0.63**	**(2.02, 4.51)**
	Open Savanna	0.82	0.44	(-0.04, 1.71)
	Open Savanna^2	**-1.16**	**0.49**	**(-2.14, -0.22)**
	Floodable	0.18	0.41	(-0.66, 0.98)
	Floodable^2	-0.46	0.43	(-1.29, 0.41)
Transit	**Intercept**	**-1.74**	**0.42**	**(-2.54, -0.92)**
	Forest	**-2.39**	**1.08**	**(-4.52, -0.38)**
	Forest^2	**2.54**	**1.21**	**(0.20, 4.93)**
	Open Savanna	**1.83**	**0.86**	**(0.22, 3.50)**
	Open Savanna^2	**-1.96**	**0.96**	**(-3.82, -0.14)**
	Floodable	0.23	0.79	(-1.37, 1.71)
	Floodable^2	0.11	0.81	(-1.44, 1.77)

Commented [R7]: What does 'itercept' mean? Is it related to the areas of transition between forest and closed savannas, as stated in the line 288?

Commented [R8]: Please consider adding a line to describe all the instances of "2" in the subtitle.

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