

1 **Human-induced changes in habitat preference by capybaras (*Hydrochoerus***
2 ***hydrochaeris*) and their potential effect on zoonotic disease transmission.**

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43

44 **Abstract**

45 Human activities are changing landscape structure and function globally, affecting
46 wildlife space use, and ultimately increasing human-wildlife conflicts and zoonotic
47 disease spread. Capybara (*Hydrochoerus hydrochaeris*) is a conflict species that has been
48 implicated in the spread and amplification of the most lethal tick-borne disease in the
49 world, the Brazilian spotted fever (BSF). Even though essential to understand the link
50 between capybaras, ticks and the BSF, many knowledge gaps still exist regarding the
51 effects of human disturbance in capybara space use. Here, we analyzed diurnal and
52 nocturnal habitat selection strategies of capybaras across natural and human-modified

53 landscapes using resource selection functions (RSF). Selection for forested habitats was
54 high across human-modified landscapes, mainly during day- periods. Across natural
55 landscapes, capybaras avoided forests during both day- and night periods. Water was
56 consistently selected across both landscapes, during day- and nighttime. This variable was
57 also the most important in predicting capybara habitat selection across natural landscapes.
58 Capybaras showed slightly higher preferences for areas near grasses/shrubs across natural
59 landscapes, and this variable was the most important in predicting capybara habitat
60 selection across human-modified landscapes. Our results demonstrate human-driven
61 variation in habitat selection strategies by capybaras. This behavioral adjustment across
62 human-modified landscapes may be related to BSF epidemiology.

63

64 **Introduction**

65 An increasing number of wild species is being forced to adapt to human-modified
66 landscapes and to live within close proximity to humans [1, 2, 3]. Across these
67 landscapes, human disturbance is linked to shifts in wildlife spatial ecology [4, 5, 6],
68 ultimately affecting zoonosis spread and transmission [7, 8]. In that context, obtain
69 accurate data to address questions on the potential effects of wild species' habitat use in
70 zoonotic disease transmission is a challenging and crucial goal to wildlife managers and
71 public health institutions.

72 Capybaras (*Hydrochoerus hydrochaeris*), the largest living rodents on the planet
73 [9], have been rising in human-modified landscapes over the last few decades [10]. These
74 semi-aquatic grazing mammals are usually found in habitats with arrangements of water
75 sources, forest patches and open areas dominated by grasses [11, 12]. Benefited by the

76 great abundance of high-quality food resources from agricultural crops and reduced
77 presence of large predators, capybara populations are recently experiencing a rapid grow
78 [11, 13].

79 Over some regions, large populations of capybaras are linked to increased crop
80 damage [14], increased vehicle collisions [15], and the spread of Brazilian spotted fever
81 (BSF) - the most lethal spotted fever rickettsioses in the world [16]. Capybaras are
82 responsible for maintaining and carrying large numbers of *Amblyomma sculptum* ticks,
83 the natural reservoir and main vector of the bacterium *Rickettsia rickettsii*, the etiological
84 agent of BSF [16]. Capybaras can also act as amplifying hosts of *R. rickettsii* among *A.*
85 *sculptum* populations [16, 17]. Even though the role of capybaras in BSF epidemiology
86 have been well-discussed [16, 17, 18, 19], little is known about the potential effects of
87 human-driven variation in capybara habitat selection to BSF spread and transmission.

88 In this study, we investigated and quantified the variation in diurnal and nocturnal
89 habitat selection strategies by GPS-tracked capybaras across natural and human-modified
90 landscapes. We tested the predictions that: (A) as other mammals (e.g. wildebeest [5]),
91 capybaras must show variation in habitat selection preferences across natural and human-
92 modified landscapes due to different levels of human disturbance in these landscapes; and
93 (B) this variation may be mainly related to temporal avoidance [20, 21] of human
94 activities in human-modified landscapes, with capybaras increasing their selection for
95 forests and water sources during daytime periods.

96

97 **Methods**

98 **Ethical statements**

99 Capybara field capture was authorized by the Brazilian Ministry of the Environment
100 (permit SISBIO No. 43259-6), by the São Paulo Forestry Institute (Cotec permit 260108-
101 000.409/2015), and approved by the Institutional Animal Care and Use Committee of the
102 Faculty of Veterinary Medicine of the University of São Paulo (protocol 5948070314).

103

104 **Study Area**

105 From 2015 to 2018, we tracked 11 groups of capybaras in Brazil with Lotek Iridium
106 Track M 2D GPS collars (Lotek Wireless, Haymarket, Ontario, CN). Of these, four
107 groups of capybaras were tracked in natural landscapes of Mato Grosso and Mato Grosso
108 do Sul states and seven groups across human-modified landscapes of São Paulo state (Fig
109 1). To assess the level of human disturbance at our study sites, we incorporated the Human
110 Footprint Index (HFI) from a previous work [22], that ranges from 0 (natural landscapes)
111 to 50 (high-density built landscapes). The spatial resolution of the global dataset is 1-km.

112 **Fig 1. Study areas across natural and human-modified landscapes in Brazil.** Study
113 sites in natural landscapes were located at Pantanal biome (green color) in Mato Grosso
114 (MT) and Mato Grosso do Sul (MS) states. Across human-modified landscapes, seven
115 study areas were located in six municipalities in São Paulo state (orange color): Ribeirão
116 Preto, Pirassununga, Araras, Americana, Piracicaba and São Paulo (Geographic
117 Coordinate System: WGS 84 / EPSG 4326).

118 For all study areas, we summarized the average HFI within the mean dispersal
119 distance of capybaras from their groups (3.4 km) at each centroid [23], calculated using

120 QGIS 2.18.9 [24]. Across natural landscapes, HFI ranged from 2.4 to 6.8 (\bar{x} = 4.5; n =
121 4), and in human-modified landscapes the index ranged from 17.4 to 37.7 (\bar{x} = 29.2; n =
122 7). In addition, Mato Grosso and Mato Grosso do Sul states have low human population
123 densities when compared to São Paulo state (Mato Grosso = 3 persons km⁻², Mato Grosso
124 do Sul = 7 persons km⁻²; São Paulo = 166 persons km⁻²) [25].

125 It is important to emphasize that no case of BSF has been reported in Mato Grosso
126 and Mato Grosso do Sul states, and serological analyses of capybaras from these natural
127 landscapes have shown no evidence of *R. rickettsii* exposure [19]. In contrast, at least
128 three study areas of human-modified landscapes in São Paulo state were classified as
129 BSF-endemic (municipalities of Americana, Araras and Piracicaba), with recent
130 occurrence of human cases and serological evidence of *R. rickettsii* infection in capybaras
131 [19].

132 Study areas in natural landscapes (São José, Ingá, Ipanema and Poconé) were
133 located in the Pantanal biome. The Pantanal is the largest wetland in the world,
134 characterized by a mosaic of upland vegetation and seasonally flooded areas [26, 27].
135 This biome consists of large areas of natural vegetation and well-structured/stable
136 ecological communities. The Pantanal support an extraordinary concentration and
137 abundance of wildlife [28], including an impressive assemblage of medium and large
138 carnivores [29, 30]. Within the sampled areas of Pantanal, capybaras had no access to
139 crops or exotic grasses.

140 Unlike natural landscapes, human-modified landscapes in São Paulo state
141 underwent significant land use and cover changes during the second half of the 19th and
142 early 20th century, transforming natural vegetation (Atlantic rainforest and Cerrado
143 biomes) into a mosaic comprised of small forest fragments surrounded by an agro-
144 pastoral matrix [31]. These forest fragments likely experience large edge effects and

145 reduced biodiversity [32], which affects the abundance of medium and large carnivores
146 across the region. Jaguar (*Panthera onca*), puma (*Puma concolor*), anacondas (*Eunectes*
147 spp.), and caimans (*Caiman* spp.) face threats in the state according to the “São Paulo
148 State Redbook of Fauna Threatened by Extinction” [33].

149 Across human-modified landscapes, we tracked capybaras in six municipalities:
150 Americana, Araras, Piracicaba, Pirassununga, Ribeirão Preto and São Paulo (Fig 1). With
151 the exception of the municipality of São Paulo, all five areas were located in agricultural
152 landscapes. Sugar cane, corn, cultivated pasturelands, and small forest fragments were
153 the dominant landscape components in the study sites. In Ribeirão Preto, the area used by
154 capybaras was surrounded by a fence that prevented animals from accessing agricultural
155 crops, but they did have access to exotic grasses, as it was also the case in the other
156 human-modified landscapes. In São Paulo municipality, capybaras were monitored in
157 Alberto Løfgren State Park, a protected area within a forest/urban matrix.

158

159 **Capybara capture and collaring**

160 In São José, Ingá and Ipanema ranches (natural landscapes), individuals were
161 tranquilized and captured with the aid of a pneumatic rifle (Dan-Inject model JM
162 Standard, Denmark). We used a mixture of ketamine (10 mg/kg) and xylazine (0.2 mg/kg)
163 to anesthetize captured animals [34]. As capybaras use water [11], we targeted animals at
164 a large distance (>20m) from this resource to reduce risk of drowning during
165 tranquilization and capture. Across all other study areas, we captured capybaras through
166 corral-type traps, similar to previously described trap [35].

167 To better understand movement of capybara populations and minimize the
168 mortality risk of tracked animals, we focused GPS collaring entirely on females. Females

169 show lower agonistic interaction rates when compared to males [36] and therefore, have
170 a decreased chance of mortality. Most female capybara are found in social groups [10,
171 37] and are thought to be philopatric [38]. We targeted the largest females within each
172 group for GPS collaring because there is a significant correlation between weight and
173 hierarchical position [36]. Hence, we assumed that dominant female movement provided
174 the best representation of group movement.

175 To avoid incorporating geolocations with large spatial errors [39], we removed GPS
176 positions with a Dilution of Precision (DOP) > 9, following recommendations in Lotek's
177 GPS collaring manual (Lotek Wireless, Haymarket, Ontario, CN.). The day of capture
178 was removed from analyses to reduce bias in space use related to capture-induced stress
179 [40]. Individuals with < 100 data points were also removed. GPS data were rarified to a
180 4-hour time interval and categorized into diurnal and nocturnal according to sunrise and
181 sunset time using the '*maptools*' package [41] in the R statistical environment [42].

182

183 **Habitat data**

184 To generate covariate data for our habitat selection analysis, we performed a
185 supervised land cover classification using Random Forests, an ensemble learning method
186 common for classifying satellite imagery [43]. We used multispectral high-resolution
187 imagery (2-m resolution) acquired by the WorldView-2 satellite (DigitalGlobe, Inc.) and
188 ancillary data derived from each satellite scene for classification (Table A in Appendix
189 S1). We established four habitat classes across natural landscapes (forest, water,
190 grasses/shrubs, bare soil) and five in human-modified landscapes (we added a
191 settlements/roads class). The land cover classification was performed using the
192 '*RStoolbox*' package [44] in the R statistical environment.

193 We digitized 1531 training polygons in QGIS 2.18.9 [24] based on visual
194 interpretation of Worldview-2 satellite scenes. Polygons were divided into calibration
195 (70%; used as input for the land cover classification) and validation (30%; used to
196 evaluate the classification). Overall accuracy ranged from 0.95 to 1 in natural landscapes
197 ($\bar{x} = 0.97$; $n = 3$) and from 0.84 to 0.99 in human-modified landscapes ($\bar{x} = 0.94$; $n = 6$).
198 We also applied a post-classification filter to reduce ‘salt-and-pepper’ noise generated by
199 per-pixel classifiers [45]. More details on the land cover classification can be found in
200 Appendix S1.

201 For each study area, we calculated the Normalized Difference Vegetation Index
202 (NDVI) [46], and created a binary classification of three habitat layers with ecological
203 relevance to capybaras: forest, water and grasses/shrubs. Forest layers included all the
204 types of forested vegetation, primary or secondary, native or not. Water layers included
205 lakes, ponds, and rivers. Grasses/shrubs layers included native and exotic underbrush and
206 shrubby vegetation, including pasturelands, and agricultural crops.

207 Using binary habitat classifications, we generated distance layers and calculated the
208 shortest distance between each capybara tracking location and habitat classes. For forest
209 distance calculations, we excluded 50-m from the forest edge to assess selection for areas
210 into the forest interior and edges as well. Large double-lane highways found at some of
211 our study sites (varying from 32 to 44 m width: Rodovia Ernesto Paterniani, Rodovia Luis
212 de Queiroz and Rodovia Anhanguera) likely present barriers to capybara’s movement.
213 Because tracked animals did not cross highways during our study, habitats located beyond
214 these highways were not included in our models. Distance to forest interior, distance to
215 water, distance to grasses/shrubs, and NDVI were used as input parameters for resource
216 selection models.

217

218 **Resource selection functions**

219 We evaluated habitat selection by comparing the use and availability of habitats
220 through a fine-scale third/fourth-order [47] resource selection function (RSF) analysis
221 [48]. Day and nighttime periods were analyzed separately, due to recognition that
222 capybara habitat use varies throughout the circadian cycle [49]. Habitat availability was
223 determined using a set of random points generated within a predetermined area, as used
224 by other colleagues [5]. We created buffers around each GPS locations with a radius equal
225 to the maximum step length displaced by each animal over a 4-hour period.

226 To determine the appropriate number of random points per ‘use’ point (GPS
227 location), we performed a sensitivity analysis following details described by previous
228 works [5, 50]. We randomly selected one individual from each study area and fit multiple
229 logistic regression models across several possibilities (1, 2, 3, 5, 10, 20, 30 and 50) of
230 random points. We repeated the process 100 times and calculated the expectation of the
231 coefficient estimates and the 95% simulation envelopes. We determined that a sample of
232 30 availability points per ‘use’ point provided stable coefficient estimates (Fig A in
233 Appendix S2). The analysis was performed in R [42].

234 We included habitat variables in our RSF after determining that they were not
235 highly correlated (Pearson’s $r > 0.65$). To facilitate comparisons across landscapes and
236 cross-time periods, we scaled and centered all data layers ($[x - \bar{x}]/\sigma_x$). We included
237 quadratic terms for all habitat variables to test for non-linear relationships. Habitat
238 selection was modeled applying a generalized linear mixed-effects logistic regression,
239 following the equation:

$$240 \quad \omega(x_i) = \exp(\beta + \beta_1 x_{1i} + \dots + \beta_n x_{ni} + \gamma_i) \quad (1)$$

241 Where $\omega(x_i)$ is the RSF, β_n is the coefficient for the n th predictor habitat variable
242 x_n , and γ is the random intercept for the animal i . We incorporated random effects into
243 the model structure to better account for differences between individuals, while also
244 accounting for unbalanced sampling designs [51]. We used nested random effects
245 (“individual” inside “study area” inside “landscape”) to evaluate landscape-level
246 coefficients. A hierarchical approach was used to account for non-independence between
247 individual movements [5]. Habitat selection was modelled using the ‘*lme4*’ package [52].

248

249 **Models**

250 We created four candidate models (forest, water, open areas and full) for each
251 landscape and time-period (Table 1) and used Akaike’s Information Criterion (AIC) to
252 rank them [53]. Models were created to evaluate the importance of different resources on
253 capybara habitat selection: (1) forest - providing shelter from daytime heat and a resting
254 place during the night [26]; (2) water - used by capybaras for thermoregulation, mating
255 and as a refuge from predator attacks [11]; and (3) open areas - used for grazing to meet
256 energy demands [49]. A fourth model, inclusive of all variables, was tested to evaluate if
257 a combination of factors most influenced capybara habitat selection.

258 **Table 1. Model structure and number of input variables (K).**

<i>Model</i>	<i>Structure</i>	<i>K</i>
Null	-	3
Forest	Distance to forest interior + (Distance to forest interior) ²	5
Water	Distance to water + (Distance to water) ²	5
Open Areas	Distance to grasses/shrubs + (distance to grasses/shrubs) ²	5

$$\text{Full} \quad \text{NDVI} + (\text{NDVI})^2 + \text{Distance to forest interior} + (\text{Distance to forest interior})^2 + \text{distance to grasses/shrubs} + (\text{Distance to grasses/shrubs})^2 + \text{Distance to water} + (\text{Distance to water})^2 \quad 11$$

259 We compared all models to a null model using chi-squared tests in R [42].
260 Coefficients of top-ranked models with confidence intervals that overlap zero were
261 considered statistically insignificant. Top-ranking models were evaluated following the
262 technique in [54], applying Spearman rank correlations between area adjusted
263 frequencies, using presence-only validation predictions and RSF bins (Appendix S3).

264

265 **Results**

266 **Capybara capture and collaring**

267 A total of 20 capybaras were captured and fitted with GPS collars. Capybaras were
268 monitored for 33 to 918 days ($\bar{x} = 273$ days), with a similar number of positions collected
269 across study areas (Table S1). Average fix success was high for both landscapes, ranging
270 from 87% to 99% in natural landscapes ($\bar{x} = 94\%;n = 4$) and from 94% to 99% in
271 human-modified landscapes ($\bar{x} = 98\%;n = 16$). Maximum distance displaced by
272 individuals in 4-hour time interval ranged from 442-m to 1437-m across natural
273 landscapes ($\bar{x} = 958.2;n = 4$) and 268-m to 2703-m in human-modified landscapes (\bar{x}
274 $= 867.6;n = 16$).

275

276 **Natural landscapes models**

277 The full model was top-ranked across day- and nighttime periods in natural
278 landscapes, indicating that all habitat variables were important in predicting capybara

279 habitat selection (Table 2). Cross-validation highlighted a strong fit to our data (Table A
 280 in Appendix S3), with stronger results for daytime periods (*day average* $r_s = 0.83$;
 281 *night average* $r_s = 0.69$). In natural landscapes, distance to water was the most
 282 important variable predicting capybara habitat selection (Table 3), with higher coefficient
 283 during nighttime periods (day: $\beta = -1.52 \pm 0.03$; night: $\beta = -1.91 \pm 0.03$; Table 3).
 284 NDVI was a weak variable in predicting capybara habitat selection during day periods
 285 and was not significant during nighttime periods (day: $\beta = 0.21 \pm 0.02$; night: $\beta =$
 286 0 ± 0.02 ; Table 3).

287 **Table 2. Model selection across natural landscapes for day- and night periods, based**
 288 **on Akaike Information Criterion (AIC).**

Model	K	AIC	ΔAIC	ω	χ^2
<i>Natural landscapes (day)</i>					
Full	11	25887.1		1	5700.4*
Forest	5	30365.4	4478.3	0	1210.1*
Open Areas	5	30982.6	5095.4	0	593.0*
Water	5	27147.5	1260.4	0	4428.1*
Null	3	31571.6	5684.4	0	
<i>Natural landscapes (night)</i>					
Full	11	23411.9		1	7598.6*
Forest	5	30073.3	6661.4	0	925.3*
Open Areas	5	30061.4	6649.5	0	937.1*
Water	5	24089.6	677.7	0	6908.9*
Null	3	30994.6	7582.6	0	

289 Models with smaller AIC values were taken as the best to predict capybara habitat
 290 selection. Top-ranked model is highlighted in bold. Likelihood ratio test (χ^2) is also
 291 displayed in table.

292 *p < 0.001

293 **Table 3. Capybara resource selection function coefficients (β) for both day- and**
 294 **nighttime across natural and human-modified landscapes.**

	<i>Natural landscapes</i>		<i>Human-modified landscapes</i>	
	<i>Day</i>	<i>Night</i>	<i>Day</i>	<i>Night</i>
NDVI	0.21 (0.02)	0 (0.02)	0.32 (0.02)	0 (0.02)
(NDVI) ²	-0.01 (0.01)	-0.03 (0)	-0.01 (0.01)	-0.15 (0.01)
Forest Interior	-0.63 (0.04)	-0.32 (0.04)	-0.83 (0.04)	-0.08 (0.03)
(Forest Interior) ²	-0.8 (0.04)	-0.72 (0.04)	0.21 (0.01)	-0.04 (0.01)
Grasses/Shrubs	0.21 (0.05)	0.02 (0.04)	1.03 (0.03)	0.57 (0.03)
(Grasses/Shrubs) ²	-0.11 (0.02)	-0.02 (0.01)	-0.36 (0.02)	-0.39 (0.02)
Water	-1.52 (0.03)	-1.91 (0.03)	-0.84 (0.02)	-0.46 (0.02)
(Water) ²	0.32 (0.02)	0.66 (0.02)	0.16 (0.01)	-0.01 (0.02)

295 Standard errors are displayed within the parentheses; Regression coefficients (β) with
 296 confidence intervals that did not overlapped zero are highlighted in boldface.

297 Capybaras selected areas further from forest interiors in natural landscapes (Fig 2),
 298 with highest probabilities of selection found in areas >250-m from the forest centroid
 299 (day- and nighttime periods). Capybaras displayed strong preferences for areas near
 300 water. This trend was consistent across day- and nighttime periods (Fig 2), with the
 301 probability of selection declining with increasing distance. Preferences for areas near
 302 open areas, dominated by grasses/shrubs, were also recorded, with probability of selection
 303 decreasing sharply at short distances (Fig 3). Probability of selection by capybaras has
 304 increased with increasing NDVI during day- and nighttime periods, although the
 305 relatively probability of selection plateaued at a NDVI value of approximately 0.5 during
 306 nighttime periods.

307 **Fig 2. Relative probability of selection of distance to forest interior and distance to**
 308 **water across natural and human-modified landscapes during day- and night**
 309 **periods.** The y axis represents the relative probability of selection, ranging from 0 to 1.

310 The x axis represents distance to the habitat. Negative values of forest graphs are related
311 to areas into the forest interior (-50m represents areas 50m inside forest patches).

312 **Fig 3. Relative probability of selection for distance to grasses/shrubs and NDVI**
313 **across natural landscapes and human-modified landscapes during day- and night**
314 **periods.** The y axis represents the relative probability of selection, ranging from 0 to 1.
315 The x axis represents the distance to grasses/shrubs or NDVI values.

316

317 **Human-modified landscapes models**

318 Across human-modified landscapes, the full model was also top-ranked for both
319 day- and nighttime periods (Table 4). Models strongly fit the data in these landscapes (
320 *day average* $r_s = 0.89$; *night average* $r_s = 0.72$), with weaker results found in São
321 Paulo municipality during nighttime, where capybaras were tracked in a non-agricultural
322 state park (Table A in Appendix S3). The most important variable in predicting capybara
323 habitat selection for day- and nighttime periods was distance to grasses/shrubs (day: $\beta =$
324 1.03 ± 0.03 ; night: $\beta = 0.57 \pm 0.03$; Table 3). Distance to water (day: $\beta =$
325 -0.84 ± 0.02 ; night: $\beta = -0.46 \pm 0.02$; Table 3) and distance to forest interior (day: $\beta =$
326 -0.83 ± 0.04 ; night: $\beta = -0.08 \pm 0.03$; Table 3) were also significant in predicting
327 capybara habitat selection, with stronger coefficients found for daytime periods. NDVI
328 was a weaker variable in predicting capybara habitat selection during daytime periods,
329 when compared to other habitat variables, and was not significant during nighttime
330 periods (day: $\beta = 0.32 \pm 0.02$; night: $\beta = 0 \pm 0.02$; Table 3).

331 **Table 4. Model selection across human-modified landscapes for day- and night**
332 **periods, based on Akaike Information Criterion (AIC).**

Model	<i>K</i>	<i>AIC</i>	ΔAIC	ω	χ^2
<i>Human-modified landscapes (day)</i>					
Full	11	40628.2		1	6678.9*
Forest	5	43675.1	3046.9	0	3620.0*
Open Areas	5	43203.9	2575.7	0	4091.2*
Water	5	45905.3	5277.1	0	1389.8*
Null	3	47291.1	6662.9	0	
<i>Human-modified landscapes (night)</i>					
Full	11	44548.5		1	259.5*
Forest	5	45984.3	1435.8	0	259.5*
Open Areas	5	45396.3	847.8	0	847.5*
Water	5	45571.3	1022.8	0	672.5*
Null	3	46239.8	1691.3	0	

333 Models with smaller AIC values were taken as the best to predict capybara habitat
 334 selection. Top-ranked model is highlighted in bold. Likelihood ratio test (χ^2) is also
 335 displayed in table.

336 *p < 0.001

337 Contrasting to natural landscapes, capybaras across human-modified landscapes
 338 were observed with higher preferences for forest interior areas and areas close to forests,
 339 with probability of selection declining with increasing distance to forested habitats (Fig
 340 2). Capybaras also showed preferences for areas near water sources, with higher selection
 341 during the day (Fig 2). Lower preferences for areas close to grasses/shrubs were found
 342 for human-modified landscapes when compared to natural landscapes, with selection
 343 increasing at mid distances (125-m) and declining at larger distances (250-m; Fig 3).
 344 Similar to natural landscapes, the relative probability of selection increased with
 345 increasing NDVI values during daytime periods (maximum coefficients at NDVI values

346 close to 0.7). For nighttime periods, the relative probability of selection peaked at a NDVI
347 value close to 0.5.

348

349 **Discussion**

350 This is the first study using GPS tracking, high-resolution imagery and resource
351 selection functions (RSF) to analyze and quantify capybara habitat selection strategies
352 across natural and human-modified landscapes. Capybaras strongly selected forested
353 habitats across human-modified landscapes, which may be a direct response to human
354 activities (e.g. agricultural machinery, people and vehicle traffic), more pronounced
355 during day periods in open areas of our study sites. As wildlife respond to human
356 disturbance following the same principles used by prey encountering predators [55],
357 capybaras may increase their selection for forests during daytime to avoid contact with
358 humans. This behavioral adaptation may be a key point in BSF epidemiology.

359 Forests are preferred ecological niche of *A. sculptum* ticks [19, 56, 57], the main
360 vectors of the BSF agent (*R. rickettsii*) [16]. In particular, environmental tick burdens
361 were found to be much higher across human-modified landscapes than across natural
362 landscapes studied here [19]. Therefore, capybaras may be highly efficient hosts across
363 human-modified landscapes, increasing their capacity in maintaining and carrying large
364 numbers of *A. sculptum* [16, 19], due to shared preferences for forested habitats.

365 As efficient vertebrate hosts for *A. sculptum* across human-modified landscapes,
366 capybaras are linked to BSF spread due to increased chance of infection by *R. rickettsii*
367 and translocation of infected ticks. Capybaras are also linked to the amplification of
368 rickettsial infection among *A. sculptum* populations, creating new cohorts of infected
369 ticks during bacteremia periods (days or weeks), when they maintain *R. rickettsii* in their

370 bloodstream [16]. In addition, *A. sculptum* populations are not able to sustain *R. rickettsii*
371 for successive generations without the creation of new infected cohorts via horizontal
372 transmission through vertebrate hosts [58, 59]. Therefore, we highlight the role of
373 capybaras selecting disturbed forest in human-modified landscapes as an important factor
374 in BSF spread.

375 Preferences for areas nearby water sources across natural and human-modified
376 landscapes were not surprising. Capybaras are semi-aquatic mammals and their
377 dependence on water sources has already been well-documented, with some authors
378 reporting these rodents hardly moving more than 500-m from water [60, 61]. However,
379 our models highlighted that capybaras were less dependent on water sources in human-
380 modified landscapes, which may be related to human-driven variation in one or more
381 behaviors linked to water use: reproduction, thermoregulation, or predator avoidance
382 [11].

383 Quality and quantity of food resources from highly nutritious agricultural and
384 pasture fields seems to have a strong influence in habitat selection by, since
385 grasses/shrubs was the strongest variable in our human-modified landscapes' models.
386 Because we wanted to compare selection for similar habitats across natural and human-
387 modified landscapes, we did not separate crops and pastures into individual habitat
388 classes. However, in the future, more detailed habitat selection studies for capybaras
389 might want to consider fine-scale spatiotemporal dynamics of agriculture and pasture
390 fields in human-modified landscapes. Understanding selection for these resources, mainly
391 sugar cane, which is linked to the BSF spread [62], may be essential to develop conflict
392 mitigation strategies for the species.

393 Lastly, improving NDVI temporal resolution could potentially increase the link
394 between this vegetation index and capybaras, since this variable was weak in predicting

395 capybara habitat selection. Higher temporal resolution of NDVI may allow for further
396 investigations on the interaction between vegetation quality and capybara habitat use.

397 Increasingly, wildlife is forced to adapt to human-modified landscapes and live
398 within proximity to humans [3]. Capybaras appear to be well adapted to anthropic
399 environments, with increased abundance and broadened distribution in Brazil [11]. This
400 is likely due to high availability of nutritious resources from agricultural crops and
401 cultivated exotic grasses, and to lower predation risk in human-modified landscapes [13].
402 The proximity between wildlife and humans has been shown to lead to increase human
403 wildlife conflicts, including zoonotic disease transfer [8]. Across human-modified
404 landscapes, large groups of capybaras have been linked to increased crop damage [14]
405 and vehicle collisions [15], as well as public health issues related to BSF spread [16].

406 Our results showed clear distinctions between habitat selection of capybaras in
407 natural and human-modified landscapes, providing a background for further investigation
408 into the potential indirect effects of human disturbance in capybara space use. The
409 development of knowledge regarding these effects may assist future management actions
410 aimed at reducing conflicts linked to the species, including those related to Brazilian
411 spotted fever (BSF) spread.

412

413 **Conclusions**

414 Through the use of GPS tracking and resource selection functions it was possible
415 to demonstrate variation in habitat selection strategies of capybaras across natural and
416 human-modified landscapes. Forested habitats were more used through human-modified
417 landscapes than across natural landscapes. In addition, capybaras consistently selected
418 areas near water in both landscapes, but this resource was more important in predicting

419 capybara habitat selection in natural landscapes. In contrast, grasses/shrubs (which
420 includes crops and pasture fields) was a stronger predictor of capybara habitat selection
421 across human-modified landscapes. Our results show the influence of anthropic
422 disturbance in capybara space use patterns. The understanding of capybara habitat use in
423 natural and human-modified landscapes may support human-wildlife conflict
424 management and Brazilian spotted fever spread control.

425

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435

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613

614 **Supporting information captions**

615 **S1 Appendix. Land cover classification of capybara habitats.** Methods on how
616 habitats of studied capybaras were classified using high-resolution satellite imagery and
617 random forest algorithm.

618 **Appendix S2. Sensitivity Analysis performed for study areas across natural and**
619 **human-modified landscapes.** We performed sensitivity analysis to set the number of
620 random points per ‘use’ point to our habitat selection models.

621 **Appendix S3. Top-ranked models’ evaluation.** We used presence-only data to evaluate
622 our top-ranked models’ performance through Spearman rank correlations between area-
623 adjusted frequencies and resource selection functions spatial bins.

624 **Table S1. Summary table for GPS-tracked capybaras across natural and human-**
625 **modified landscapes.**

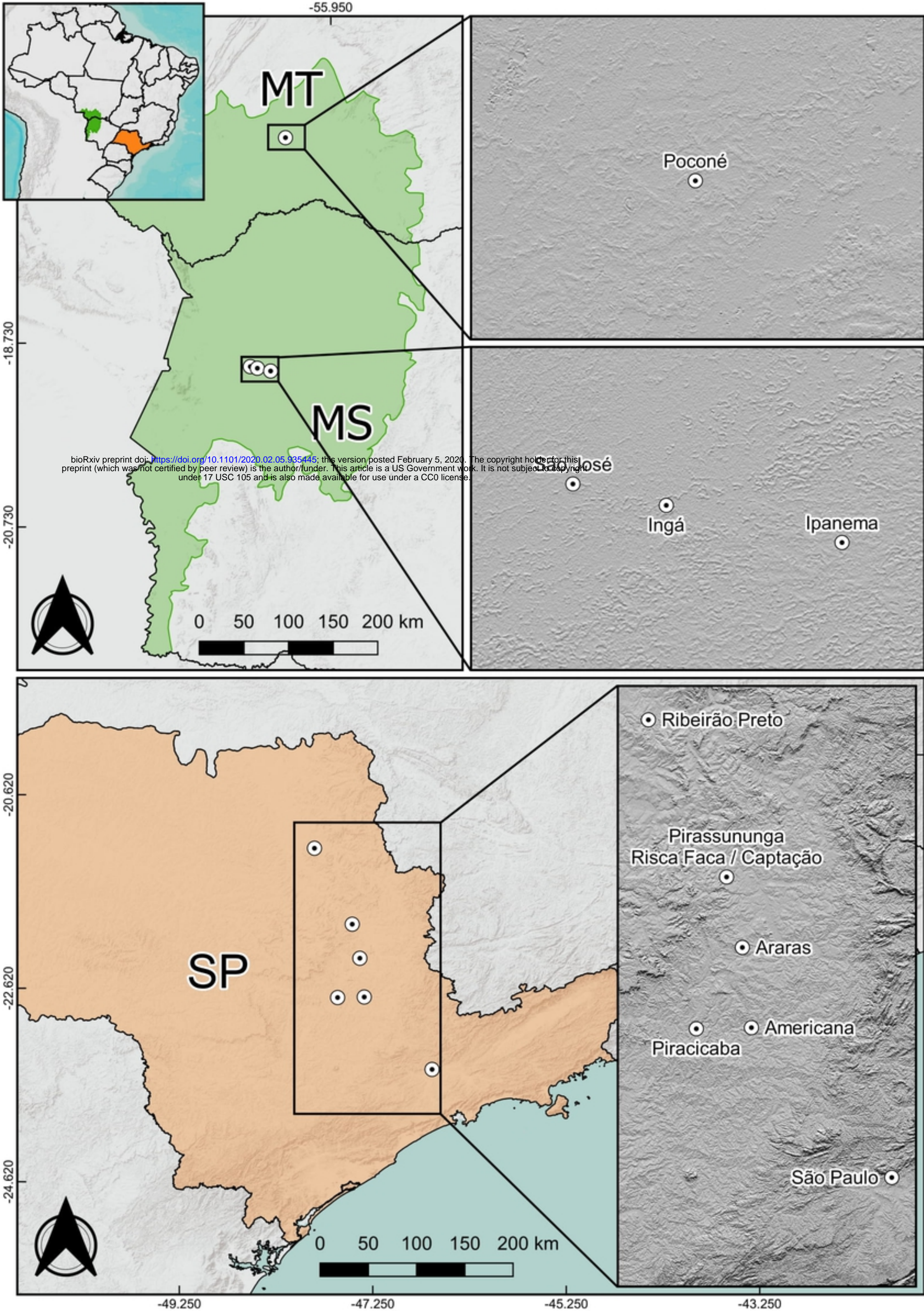
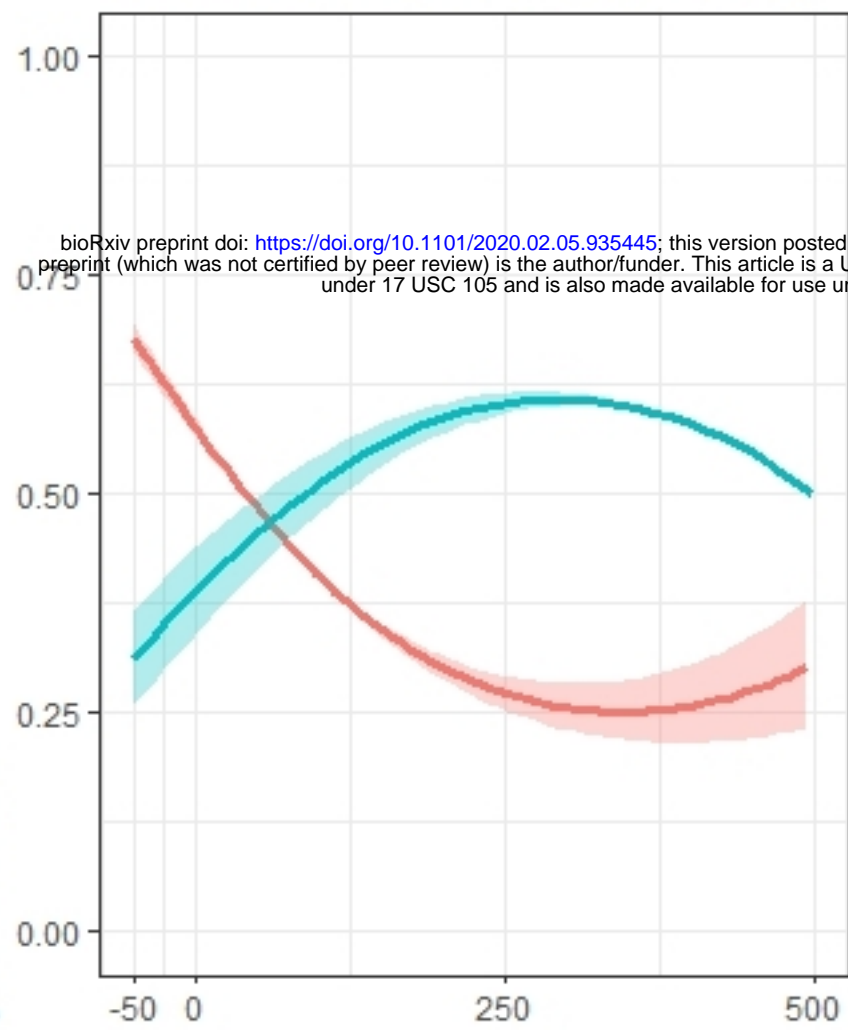
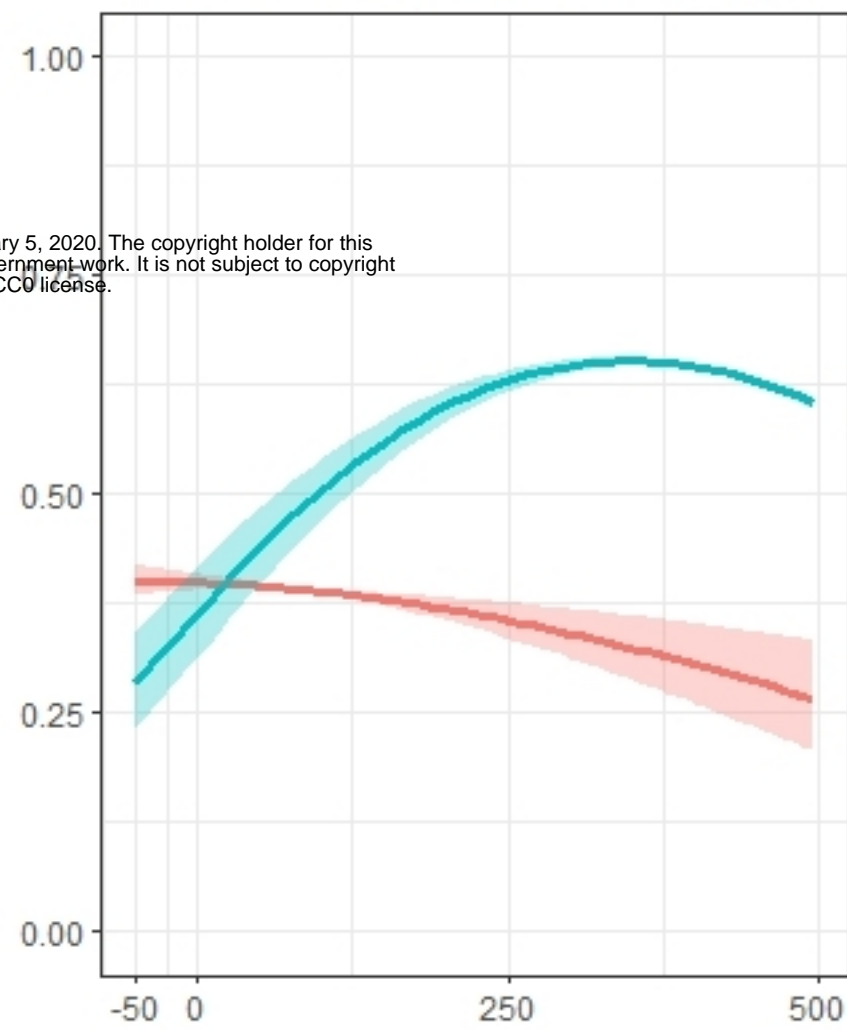


Fig 1

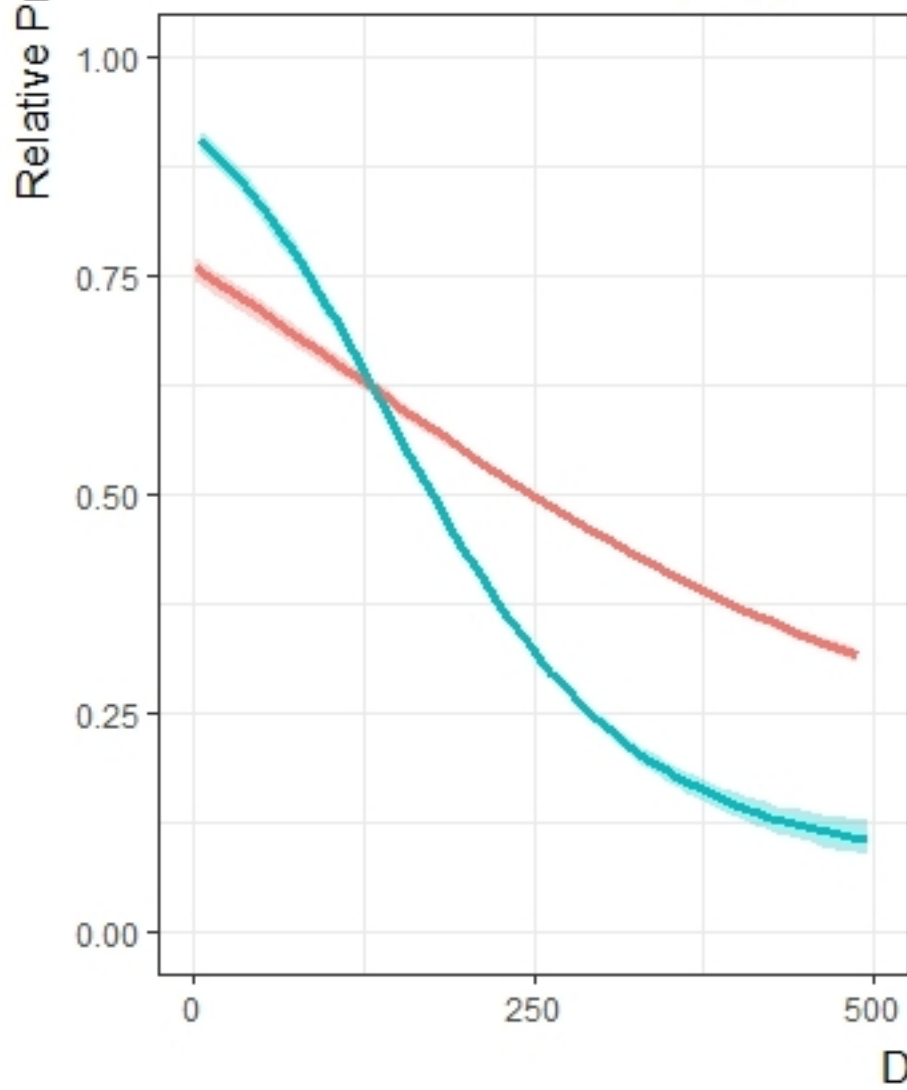
Distance to Forest Interior (Day)



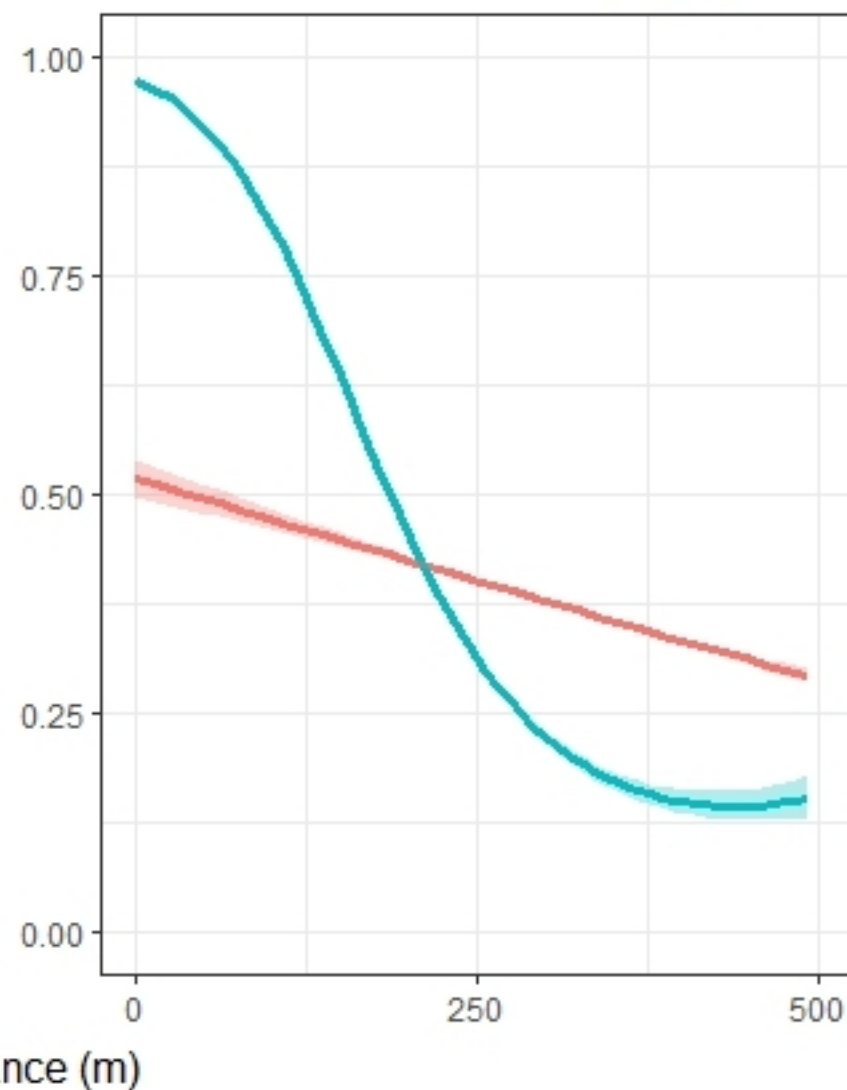
Distance to Forest Interior (Night)



Distance to Water (Day)



Distance to Water (Night)



Landscape

- HMLs
- NLs

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Fig 2

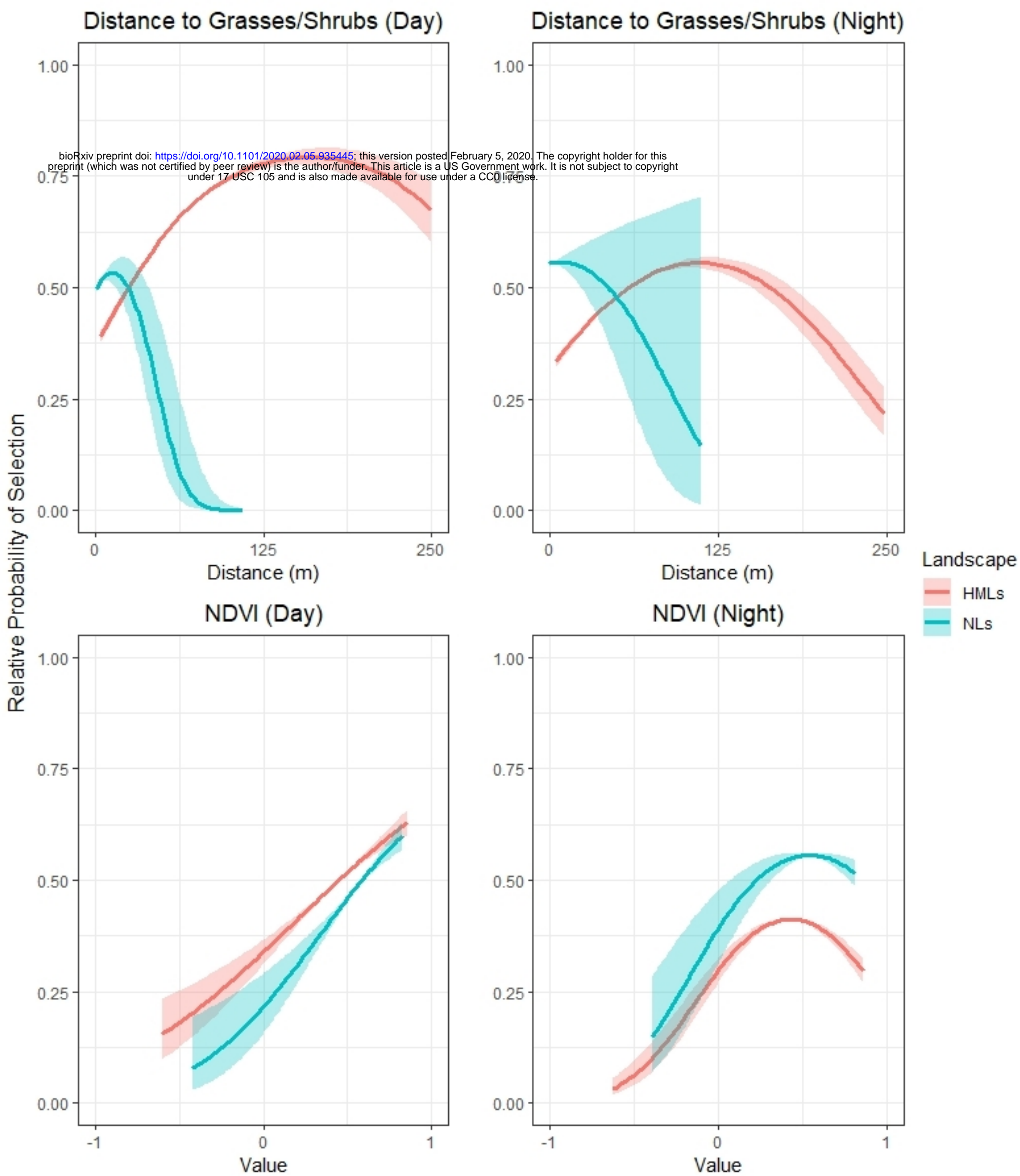


Fig 3