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Home range and habitat data for Hispaniolan mammals challenge assumptions for conservation management

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1 **Home range and habitat data for Hispaniolan mammals**  
2 **challenge assumptions for conservation management**

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18 **Abstract.** Conservation decision-making for threatened species in human-  
19 modified landscapes requires detailed knowledge about spatial ecology, but  
20 robust data derived from tracking individual animals are often unavailable, with  
21 management decisions potentially based on unreliable anecdotal data. Existing  
22 data are limited for Hispaniola's two threatened non-volant land mammals, the  
23 Hispaniolan hutia (*Plagiodontia aedium*) and Hispaniolan solenodon (*Solenodon*  
24 *paradoxus*), with assumptions that hutias are better able to tolerate landscape  
25 disturbance. We collected spatial behaviour and habitat use data for Hispaniolan  
26 mammals during a multi-year field programme across undisturbed and modified  
27 habitats in southwestern Dominican Republic, using GPS units for hutias (11  
28 individuals) and radio-telemetry for solenodons (22 individuals). Although  
29 significant differences exist in hutia home range estimates between different GPS  
30 error derivation strategies and estimated terrestrial/arboreal behaviour  
31 scenarios (95% KDE means=23,582-28,612m<sup>2</sup>), hutias almost exclusively use  
32 forest under all estimates (mean observations in forest across all  
33 strategies/scenarios=90.3%, total range=69.1-100%). Solenodons have larger  
34 estimated home ranges (95% KDE mean=156,700m<sup>2</sup>), with differences between  
35 wet and dry season estimates, and show much more variation in habitat use than  
36 hutias within the same landscape; animals regularly use both forested and  
37 modified habitats, being observed most frequently in forest (mean=74.0%,  
38 range=13.0-99.1%) but also occurring regularly in pasture (mean=15.9%,  
39 range=0-80.0%) and cropland (mean=7.7%, range=0-62.0%), and den in all  
40 three habitats. This new baseline on Hispaniolan mammal spatial ecology  
41 challenges anecdotal data, and suggests solenodons may be better able to  
42 tolerate disturbance and persist in modified landscapes.

43

44 **Keywords.** Dominican Republic; evidence-based conservation; hutia; Kernel

45 Density Estimate; solenodon; telemetry

ACCEPTED MANUSCRIPT

**46 1. INTRODUCTION**

47 Effective conservation management and decision-making for threatened species  
48 requires an evidence-based approach, informed by robust empirical data on key  
49 population parameters (Sutherland et al., 2004; Segan et al., 2011). In particular,  
50 it is crucial for conservation biologists to have a detailed understanding of the  
51 spatial movements and habitat use of threatened species. Tracking individual  
52 animals to collect spatial-use data can provide answers to key ecological  
53 questions about intraspecific, interspecific, and ecosystem-level interactions  
54 (Powell, 2000; Fieberg et al., 2010). Such information is particularly important  
55 for species in modified and fragmented landscapes, where assessing utilisation of  
56 different natural and non-natural habitats can determine population viability,  
57 integrate demands on land, and direct protected area designation (Fagan and  
58 Lutscher, 2006; Sawyer et al., 2009). However, robust datasets are often  
59 unavailable for poorly-known, elusive species of conservation concern. Decision-  
60 making for such species can be forced to rely on limited, non-systematic and  
61 potentially unreliable “anecdotal” data, which can lead to biological  
62 misunderstanding and misdirection of conservation efforts (McKelvey et al.,  
63 2008).

64 The insular Caribbean formerly contained a diverse species-rich assemblage  
65 of endemic land mammals, but nearly all of this fauna became extinct during the  
66 world’s largest postglacial mammal extinction event, with species losses  
67 probably associated with human activities (hunting, landscape transformation,  
68 invasive mammal introduction) from the mid-Holocene into the historical period  
69 (Cooke et al., 2017). Most of the few surviving species are threatened with  
70 extinction (Turvey et al., 2017). Hispaniola, the second-largest Caribbean island

71 (divided politically into the Dominican Republic and Haiti), retains only two non-  
72 volant native land mammals, both representatives of endemic Caribbean  
73 families: the Hispaniolan solenodon (*Solenodon paradoxus*), a large eulipotyphlan  
74 insectivore, and the Hispaniolan hutia (*Plagiodontia aedium*), a large capromyid  
75 rodent (Fig. 1). Both species have been considered rare and in danger of  
76 extinction, if not already extinct, since the nineteenth century (Cuvier, 1836;  
77 Verrill, 1907; Allen, 1942; Fisher and Blomberg, 2011). They are both listed as  
78 Endangered by IUCN (2018), and recognised as global conservation priorities  
79 based on evolutionary distinctiveness (Collen et al., 2011).

80 The biology and ecology of Hispaniolan mammals are poorly understood,  
81 due to their apparent rarity, secretive nocturnal behaviour, and occurrence in  
82 rugged limestone landscapes. Both species have generalist diets, and den in small  
83 groups, probably comprising pair-bonded and related individuals including  
84 parents and offspring from multiple litters (Sullivan, 1983; Ottenwalder, 1991,  
85 1999; Woods & Ottenwalder, 1992). However, existing data about spatial  
86 movements and habitat use are limited, with no information on key parameters  
87 such as home range, and such data are only available from studies that usually  
88 failed to report survey effort or field methods, or provide analyses or  
89 quantitative results. Previous studies focused on investigating native mammal  
90 occurrence in different natural vegetation types across Hispaniola. Older studies  
91 concluded that both species were associated with broadleaf forest containing  
92 rocky crevices for denning, with no indication of differences in habitat selectivity  
93 between species (Sullivan, 1983; Woods and Ottenwalder, 1992; Ottenwalder,  
94 1999). Recent country-wide analysis of occurrence inside protected areas  
95 suggests that hutias are more dependent than solenodons upon rocky substrate

96 for dens (Kennerley et al., 2019). Ecological inferences about Hispaniolan  
97 mammals based on phylogenetic comparisons with related species also provide  
98 only limited insights. *Plagiodontia* is the sister taxon to all other living hutias  
99 (Fabre et al., 2014), which include both habitat specialists (e.g. mangrove-  
100 specialist dwarf hutias *Mesocapromys*) and ecological generalists found across  
101 multiple land-cover types (e.g. Desmarest's hutia *Capromys pilorides*), and which  
102 exhibit varying levels of obligate arboreal behaviour and restriction to forested  
103 environments (e.g. prehensile-tailed hutia *Mysateles prehensilis* versus ground  
104 hutias *Geocapromys*) (Clough, 1972; Borroto-Páez & Mancina, 2011). The other  
105 surviving solenodon species, the Cuban solenodon (*Atopogale cubana*), is largely  
106 restricted to montane and submontane primary forest, although this represents  
107 a remnant distribution (Borroto-Páez & Mancina, 2011).

108       Although ongoing forest loss is occurring across Hispaniola (Pasachnik et al.,  
109 2016), native mammal tolerance of habitat modification has not been rigorously  
110 investigated. Both species have been reported anecdotally from disturbed  
111 secondary forest or partially deforested landscapes, suggesting they might  
112 persist at least temporarily under some level of disturbance if suitable rocky  
113 crevices are available, and Turvey et al. (2017) recently proposed that both  
114 species should be downlisted to Near Threatened by IUCN because there is no  
115 evidence of recent subpopulation declines or extirpations. However, populations  
116 are considered at high risk of extirpation if disturbance is not reduced and  
117 vegetation does not enter successional recovery (Sullivan, 1983; Woods, 1983;  
118 Ottenwalder, 1999). The only previous study to consider relative resilience of  
119 Hispaniolan mammals to habitat loss was conducted in southwestern Haiti by  
120 Woods (1981), who concluded from opportunistic collection records and local

121 reports that hutias were locally more abundant than solenodons in modified  
122 landscapes and appeared better-suited to tolerate disturbance, possibly due to  
123 more general habitat preferences.

124 Robust data on basic biological and ecological parameters remain  
125 unavailable for most surviving Caribbean mammals (Turvey et al., 2017).  
126 Anecdotal data for several Caribbean species have proved to be erroneous or  
127 misinterpreted, with such mistakes having hindered effective conservation  
128 planning (Baisre, 2016; Young et al., 2018). In order to strengthen the evidence-  
129 base for Caribbean mammal conservation and reduce the risk that management  
130 decisions are guided by limited or inadequate data, we conducted a long-term  
131 field project on Hispaniolan solenodons and hutias to investigate spatial  
132 behaviour and habitat use across both undisturbed and modified habitats. We  
133 calculated size, variation, and composition of Hispaniolan mammal home ranges,  
134 and specifically tested predictions based on Woods (1981) that hutias might be  
135 expected to show greater utilisation of modified habitats compared to  
136 solenodons in other Hispaniolan landscapes. Our findings challenge previous  
137 assumptions about the ecology of these two poorly-known threatened species,  
138 and provide an important new baseline for understanding resilience and  
139 responses of Caribbean mammals to environmental change.

140

## 141 **2. MATERIAL AND METHODS**

142

### 143 **2.1. Study sites**

144 Fieldwork was conducted in February 2011-February 2013 near small rural  
145 communities in two unprotected landscapes in the southern Sierra de Bahoruco



146 mountains, Pedernales Province, southwestern Dominican Republic: (1) Mencia  
147 (18°10'10N, 71°44'25W), elevation=300-450m; (2) Las Mercedes (18°05'13N,  
148 71°39'55W), elevation=270-440m (Fig. 1). Rainfall data during the study period  
149 from Movebank (Dodge et al., 2013) show that December-March are the driest  
150 months. Weather data from Pedernales show little variation in monthly average  
151 temperatures (mean monthly highs $\pm$ SE=24.17 $\pm$ 1.80°C; mean monthly  
152 lows $\pm$ SE=18.83 $\pm$ 1.34°C) (data from <http://www.worldweatheronline.com/>).

153 Field sites were selected because they contain a mosaic of (1) tropical  
154 broadleaf forest (mainly dry secondary forest, with primary semi-humid forest  
155 along river gorges; both with thick leaf litter, thin ground flora and some scrub  
156 layer), and (2) modified habitats (either containing no remaining forest, or with  
157 forest used for cultivation, e.g. shade-grown coffee), within a limestone karst  
158 landscape. These broad habitat types are easily distinguishable in the field, and  
159 clear boundaries between habitat types often exist (e.g. fences). Habitat maps  
160 were constructed by mapping perimeters of forest patches (defined as trees >5m  
161 tall with closed canopy), pasture, cropland (cash-crop plantations, subsistence  
162 agriculture) and human habitat (roads, houses, manmade structures) on foot  
163 using a handheld GPSmap 60CSx (Garmin, KA, USA) set to record fixes every  
164 second; data were combined with Google Earth images to map permanent  
165 boundaries such as roads, and form contiguous habitat maps using ArcMap 10  
166 (ESRI, 2013).

167 All habitats were visited in daytime to locate dens and species-specific signs  
168 (Kennerley et al., 2019). Areas where signs were detected were revisited at  
169 night. Animals were located by listening for sounds of foraging/movement, and  
170 were caught by hand. They were microchipped in the nape using ID-162 FDX-B

171 transponders (1.4×8mm; ZooChip, The Pet Chip Company Ltd, London, UK), and  
172 weight, sex, and number of other observed individuals was recorded. No  
173 anaesthetics were used. All animal handling/collaring procedures were  
174 approved by the Durrell Wildlife Conservation Trust ethics committee.

175

## 176 **2.2. Spatial behaviour**

177

### 178 **2.2.1. Hutia**

179 Animals were studied at Mencia in November 2011-February 2013. An i-gotU  
180 GPS Travel & Sports Logger GT-120 (Mobile Action Technology Inc., Taiwan)  
181 with modified built-in patch antenna was deployed on each individual using neck  
182 collars surrounded with soft tubing. Modifications included: use of Extreme  
183 LP1S500 battery (3.7V 500mAh Lithium Polymer); circuit board strengthened  
184 using Araldite epoxy; weatherproofing with clear plastic coating (PlastiDip, UK);  
185 GPS components rehoused in hard 20×46×32mm Camdenboss RX2007/S-5 box  
186 (Premier Farnell, UK) with drainage holes. A 23g TW-3 medium mammal tag  
187 VHF radio transmitter with whip aerial (Biotrack Ltd., Dorset, UK) was attached  
188 to the collar to allow tracking of individuals with a hand-held Yagi 3-element  
189 antenna and Sika radio receiver (Biotrack Ltd., Dorset, UK) for welfare  
190 monitoring and collar retrieval. Seven units were used. Modified GPS units  
191 weighed 35g and the total collar+tag weighed 56g; this is 4.2% of mean adult  
192 body mass in the study area (see section 3.1.1), with collars only deployed on  
193 individuals where this was <5% of body mass. Units were programmed with a  
194 two-night delayed start, to allow animals to habituate to collars and revert to  
195 normal behaviour. Units were subsequently scheduled to record fixes (date, time,

196 longitude, latitude, altitude) at 30-minute intervals between 9pm-5am (i.e.  
197 excluding periods when animals were in dens), reverting to sleep mode between  
198 fixes to extend battery life. Data were stored using built-in memory of 16Mb.  
199 Collars were retrieved after six weeks.

200

### 201 **2.2.2. Solenodon**

202 Neck collars carrying 13g MicroTraX™ Tag GPS units (Alana Ecology Ltd., UK)  
203 were trialled on six individuals during a pilot study in Mencia (February-July  
204 2011), with all collars+tags <5% body mass. Regular health checks revealed that  
205 although animals showed no visible signs of harm, several lost weight (mean=  
206 47g over 3-7 days, n=3) and units were damaged by denning in limestone  
207 crevices, so radio-telemetry was employed as an alternative method.

208 Estimation of positional accuracy associated with triangulation in different  
209 habitats was conducted at Las Mercedes. Fifteen pairs of random points 100m  
210 apart were generated in forest, pasture and cropland, the radio-collar was placed  
211 at one paired point, and telemetry was conducted from the other paired point to  
212 estimate radio-collar position with two GPS points and two bearings. Remote  
213 cameras (Moultrie I-60, Moultrie Feeders, Calera, U.S.A.; Ltl Acorn 5210A 12MP,  
214 LTL Acorn Outdoors, Green Bay, U.S.A.) were placed at occupied den entrances  
215 during the pilot study to determine behavioural patterns, with 84 records (41  
216 individuals leaving dens, 43 returning to dens) collected across 61 nights (7pm-  
217 7am). Solenodons were less active above ground during the first 90 min after  
218 sunset and last 90 min before sunrise, so these periods were excluded from the  
219 subsequent tracking schedule (Supporting Information Fig. S1).

220 Three periods of tag deployment and telemetry were conducted: Mencia dry  
221 season (30 November 2011-25 January 2012); Las Mercedes wet season (10  
222 April 2012-1 June 2012); Las Mercedes dry season (17 December 2012-19  
223 February 2013). Individuals were targeted from different groups within seasons  
224 if possible, and during the Las Mercedes dry season, attempts were made to  
225 recapture individuals from wet season groups. Triangulation was conducted  
226 after moving signals were detected, to confirm animals had left dens. Point  
227 sampling was used, with a single location fix per individual per night to avoid  
228 autocorrelation (Kenward, 2001). Animals were approached from good vantage  
229 points to a distance of ~100m (determined by signal strength), with location  
230 fixes (GPS coordinate/bearing) taken at two points >50m apart. All tagged  
231 individuals were located each night within less than two hours to confirm they  
232 were not foraging together, and were not sampled within the same time period  
233 on consecutive nights. Den checks were made every ~10 days at Mencia and  
234 three times/week at Las Mercedes. Individuals <800g were recaptured for health  
235 checks halfway through each period, with location fixes not collected the  
236 following night. All collars were retrieved at the end of each period.

237

### 238 **2.3. Home ranges**

239 Statistical analyses were performed in R v3.0.1 (R Development Core Team,  
240 2013).

241

#### 242 **2.3.1. Hutia**

243 Tracking fixes were screened for outliers by excluding locations for which speeds  
244 >2 standard deviations above mean trip speed were necessary between

245 successive fixes (Bjørneraas et al., 2010). Brownian Bridge Movement Models  
246 (BBMMs) based on the temporal structure of tracking data were used to  
247 calculate home ranges; these enable analysis of data containing temporal  
248 autocorrelation, and with GPS error incorporated directly into models to give  
249 single values for all points in a track (Horne et al., 2007). Utilisation Distributions  
250 (UD; probability density of relocating individuals at any location) for each nightly  
251 trip of a hutia were produced using the 'BBMM' package in R v3.0.1 (Nielson et  
252 al., 2013); these were combined and averaged to produce single UDs for each  
253 hutia over the tracking period, from which 95% volume contours were  
254 calculated (defining areas containing 95% probability of finding individuals;  
255 Fieberg, 2007).

256 Error tests were conducted on stationary GPS units to calculate FSR (number  
257 of successful fixes/scheduled fixes) and ME (Euclidean distance between fix  
258 position and known reference position, calculated from five location  
259 measurements from handheld GPS), with units scheduled to take fixes at 30min  
260 intervals over a 24hr period with antennae facing upwards. There was no  
261 significant difference in inherent error of ME between units when placed 10cm  
262 above the ground in an open area (mean±SE=9.98±8.84m; one-way ANOVA,  
263  $F_{(6,298)}=0.629, p=0.701$ ); a single unit was used in all subsequent stationary tests.  
264 At three randomly generated forest points within a 150m radius of each hutia  
265 study den, error testing was then conducted at both ground-level and canopy-  
266 level (mean GPS height in tree±SE=8.2±2.3m, range=4-13m).

267 The influence of topography and ground/canopy position on ME was  
268 modelled using linear mixed models (LMM) with Gaussian error distribution,  
269 with stationary test points included as random intercepts to account for non-

270 independence of repeated MEs at each location. Sky availability was calculated  
271 for each point at ground and canopy positions in ArcMap (ESRI, 2013) using the  
272 Skyline Graph tool and a 30m resolution ASTER Global Digital Elevation Model  
273 (DEM) of the Dominican Republic (METI and NASA, 2011). Input variables were  
274 scaled to a mean of zero and SD=0.5. A global model including an interaction  
275 term between sky and position, and all possible sub-models, were ranked by  
276 Akaike's Information Criterion (AIC); parameter estimates were averaged across  
277 all models with  $\Delta AIC \leq 6$ , including zeros as coefficients when variables did not  
278 enter particular models (Burnham and Anderson, 2002). Analyses were re-run  
279 using the SD of ME at each fix point as the response variable, with models  
280 compared using Akaike's second-order corrected Information Criterion (AIC<sub>c</sub>)  
281 for small sample sizes.

282 To explore the interaction between ME and foraging behaviour on home  
283 range estimates, three error derivation strategies were used to calculate and  
284 assign SDs to fixes: **1**, "unit error" (mean SD from GPS unit error testing); **2**,  
285 "landscape error" (mean SD across all ground and all canopy forest tests,  
286 incorporating effects of topography and vertical position but generalising these  
287 errors across study site); **3**, "point error" (SD for each point predicted from  
288 model-averaged parameter estimates in the SD model above and mapped across  
289 study site at both ground and canopy level). For point error, sky availability was  
290 calculated for each 30m cell using the DEM, canopy estimates were based on  
291 mean GPS height in canopy stationary tests, and maps were rasterised using  
292 ArcMap and hutia tracking data were overlain to identify values for each  
293 location.

294 Home range estimates were derived for five behaviour scenarios: movement  
295 entirely on ground or in canopy, or with fixes randomly assigned to generate  
296 track proportions of 75% ground:25% canopy, 50% ground:50% canopy, or 25%  
297 ground:75% canopy, with random point allocation iterated 10 times. Scenarios  
298 were repeated using predicted ground and canopy SD error values; any points  
299 that fell outside the forest habitat layer were assigned a mean SD from GPS  
300 error-testing. UDs were produced for each scenario and combined into a single  
301 nightly UD. Differences between strategies and scenarios were investigated with  
302 repeated measures ANOVAs and paired t-tests.

303

### 304 **2.3.2. Solenodon**

305 UDs were obtained using Kernel Density Estimates (KDE; Worton, 1989),  
306 calculated for each individual with Geospatial Modelling Environment (Beyer,  
307 2012) using 5m cell size and an automated plug-in estimator algorithm  
308 (Sheather and Jones, 1991), from which 95% volume contours were calculated.  
309 Asymptote analysis was conducted to assess whether sufficient fixes were  
310 available to determine home range. For each individual, 10 points were  
311 randomly sampled 50 times from the complete pool of fixes, and home range  
312 mean and 95% CI were estimated using KDE; this process was repeated up to the  
313 total number of fixes, with data considered sufficient if the five preceding  
314 estimates fell within 10% of the mean home range estimated from the full  
315 dataset (Laver and Kelly, 2008).

316 Influence of group size (estimated using camera traps and field  
317 observations), study site and season (wet/dry) on home range was modelled  
318 using LMM with Gaussian error distribution and identity link. Group ID was

319 included as a random term. Input variables were scaled to a mean of zero and  
320 SD=0.5. A global model including only main effects, and all possible sub-models,  
321 were ranked by AIC<sub>c</sub>.

322

#### 323 **2.4. Habitat use**

324 Habitat utilisation and selection by both species was analysed using habitat  
325 compositional analysis (Aebischer et al., 1993) in the 'adehabitat' package in R  
326 (Calenge, 2006), at two levels: **1**, selection of home ranges within study area was  
327 quantified by comparing home range habitat composition with composition of  
328 available habitat within each season (Second Order selection; Johnson, 1980); **2**,  
329 where data allowed, selection of fixes within home ranges was quantified by  
330 comparing the proportion of active fixes in each habitat with availability of each  
331 habitat (Third Order selection).

332 Areas of different available habitats were calculated within 232m buffers  
333 (hutias) or 522m buffers (solenodons) around all recorded dens and radio-  
334 telemetry/GPS locations (maximum Euclidean distance travelled in one night  
335 from den to radio-telemetry/GPS fix). Zero values were replaced by values of  
336 0.01 (Aebischer et al., 1993). Analysis was conducted using only one individual  
337 tracked from a group, or only one tracking period if an individual was tracked  
338 during multiple seasons, to ensure data independence. Significance of habitat  
339 selection was tested using MANOVA with the Wilks' lambda ( $\lambda$ ) statistic, using  
340 matrices to indicate direction of habitat preference (Aebischer et al., 1993).

341

### 342 **3. RESULTS**

343



### 344 **3.1. Fieldwork summary**

345

#### 346 **3.1.1. Hutia**

347 Collars were deployed 18 times, with data retrieved successfully on 12 occasions  
348 from 11 individuals (7♂, 4♀) from 11 groups. Deployments contained 20-35  
349 night cycles of data. Group size ranged between 2-6 observed individuals  
350 (mean=3.2). Adult males had a mean body mass of 1322.9g (n=12, range=1040-  
351 1795g), and adult females had a mean body mass of 1355.0g (n=5, range=1180-  
352 1530g); total mean body mass for all individuals was 1335.0g (n=17). GPS data  
353 show all study animals used the same dens throughout the survey period.

354

#### 355 **3.1.2. Solenodon**

356 Collars were deployed 28 times, with 22 individuals (9♂, 13♀) from 18 groups  
357 tracked successfully for the full period (>30 fixes obtained). Group size ranged  
358 between 1-5 observed individuals (mean=2.8). Adult males had a mean body  
359 mass of 889.6g (n=12, range=720-1070g), and adult females had a mean body  
360 mass of 849.7g (n=16, range=600-1090g); total mean body mass for all  
361 individuals was 866.8g (n=28). During the survey period, all study individuals  
362 changed dens (number of observed dens used per season=2-12, mean=4.8); dens  
363 were identified as different if they had distinct above-ground entrances with no  
364 obvious connectedness, although the region's limestone landscape might support  
365 large underground den complexes with multiple entrances. Individuals from the  
366 same group were regularly heard and observed foraging together and using the  
367 same dens.

368

## 369 3.2. Home ranges

370

### 371 3.2.1. Hutia

372 A total of 3311 fixes were obtained (mean $\pm$ SE=276 $\pm$ 82), with mean FSR of 65%  
373 (SE=11.9%). In error testing, mean FSR was 99.4% (SE $\pm$ 1.0%, range=97.9-  
374 100%) in open tests and 83.3% (SE $\pm$ 12.8%, range=43.8-100%) across all forest  
375 tests, with a significant difference between position of unit in canopy  
376 (mean $\pm$ SE=87.9 $\pm$ 8.7%) versus ground (mean $\pm$ SE=78.7 $\pm$ 14.3%;  $t=6.157$ ,  
377  $p<0.001$ ). Model selection revealed three plausible models explaining differences  
378 in ME and four plausible models explaining differences in SD; both ME and SD  
379 increased on the ground and with decreasing sky availability, and with an  
380 interaction between position and sky showing that increasing sky availability  
381 reduced ME to a greater extent for units on the ground (Table 1).

382 Home range estimates for hutia individuals varied significantly depending  
383 on error derivation strategy and behaviour scenario (Fig. 2; Supporting  
384 Information Fig. S2, Table S1). BBMMs parameterised using unit error produced  
385 the smallest estimates (mean=23,582m<sup>2</sup>). For the other methods, estimates  
386 increased across the five scenarios as the ratio of canopy fixes to ground fixes  
387 increased, and BBMMs parameterised using landscape errors usually produced  
388 smaller estimates (means=25,418-27,690m<sup>2</sup>) compared to point errors  
389 (means=26,253-28,612m<sup>2</sup>). There was no spatial overlap between home ranges  
390 of different individuals, irrespective of strategy/scenario estimation method.

391

### 392 3.2.2. Solenodon

393 Home ranges were estimated for six individuals (4♂, 2♀) in Mencia, ten  
394 individuals (3♂, 7♀) in wet season at Las Mercedes, and six individuals (2♂, 4♀)  
395 in dry season at Las Mercedes, with individuals from three groups tracked in  
396 both seasons at Las Mercedes (Fig. 3; Supporting Information Fig. S3). There was  
397 no significant difference in VHF error measurements between habitats (ANOVA,  
398  $F_{(2,42)}=1.4586, p=0.2441$ ; mean error distance across habitats $\pm$ SE=5.38 $\pm$ 0.39m).  
399 Asymptote analyses indicate sufficient data for home range estimation were  
400 collected for all individuals.

401 The mean 95% KDE was 156,700m<sup>2</sup> (SD $\pm$ 81,758m<sup>2</sup>). AIC<sub>c</sub> produced a single  
402 top model containing season as the only predictor and group ID as random effect,  
403 with  $R^2_{\text{GLMM (m)}}=0.37$  and  $R^2_{\text{GLMM (c)}}=0.68$  indicating good fit and explanatory  
404 power. Based on parameter estimates from this model, home ranges are larger in  
405 the wet season (213,423m<sup>2</sup>) than the dry season (117,900m<sup>2</sup>).

406

### 407 3.3. Habitat use

408

#### 409 3.3.1. Hutia

410 Despite significant differences in predicted home range across strategies and  
411 scenarios, there were only relatively small changes in habitat composition within  
412 home ranges (Fig. 2; Supporting Information Fig. S2). Hutia were largely  
413 restricted to forest (mean across all strategies/scenarios=90.3%,  
414 strategy/scenario mean range=88.6-91.5%, total range=69.1-100%), with  
415 limited occurrence in pasture (overall mean=7.3%, mean range=6.5-8.3%, total  
416 range=0-30.9%) and minimal occurrence in cropland (overall mean=1.9%, mean

417 range=1.5-2.4%, total range=0-11.6%) or human habitat (overall mean=0.6%,  
418 mean range=0.5-0.6%, total range=0-5.1%). All recorded dens were in forest.

419 Habitat composition within pooled ranges was significantly different from  
420 composition of available habitat ( $\lambda < 0.001$ ,  $p < 0.001$ ). Forest was used  
421 significantly more than crop, pasture, and human habitats. Although human  
422 habitat was included within home range boundaries, no fixes occurred within  
423 this habitat.

424

### 425 3.3.2. *Solenodon*

426 Individuals showed much more variation in habitat use compared to hutias (Fig.  
427 3; Supporting Information Fig. S3-S4). Most frequent overall occurrence was in  
428 forest (mean=74.0%, range=13.0-99.1%), but animals were also observed  
429 frequently in pasture (mean=15.9%, range=0-80.0%) and cropland (mean=7.7%,  
430 range=0-62.0%), with little occurrence in human habitat (mean=2.3%, range=0-  
431 6.8%). Of 102 recorded dens across both sites and all seasons, 80 were in forest,  
432 18 in pasture, and four in cropland. Only 11 groups denned exclusively in forest,  
433 and four groups denned exclusively in non-forest habitats (three exclusively in  
434 pasture, one in both pasture and cropland).

435 Habitat composition within pooled ranges was significantly different from  
436 composition of available habitat in all seasons (Mencia,  $\lambda = 0.05$ ,  $p = 0.002$  or  
437  $\lambda = 0.06$ ,  $p = 0.003$ , depending on which individual from same group is used in  
438 pooled analysis; Las Mercedes wet season,  $\lambda = 0.20$ ,  $p = 0.001$ ; Las Mercedes dry  
439 season,  $\lambda = 0.18$ ,  $p = 0.017$ ). At Mencia (dry season), forest was included within  
440 predicted home range significantly more than cropland or human habitat, and  
441 pasture was included significantly more than cropland. At Las Mercedes, forest

442 and human habitat were included significantly more than pasture or cropland in  
443 the wet season, and forest and human habitat were included significantly more  
444 than pasture in the dry season. Selection of fixes within home ranges was only  
445 possible for wet season at Las Mercedes, and showed that fixes occurred  
446 significantly more often in forest, pasture and cropland compared to human  
447 habitat.

448

#### 449 **4. DISCUSSION**

450 Our study provides the first systematically-derived estimates of home range and  
451 landscape-level habitat use for any insular Caribbean mammals, and the first  
452 such data for any representatives of the endemic and highly threatened  
453 Caribbean families Capromyidae or Solenodontidae. These species provide many  
454 challenges to research due to their secretive nocturnal habits and perceived  
455 rarity; previous studies of spatial ecology for Caribbean land mammals have  
456 been restricted to qualitative assessment of presence in habitats or altitudinal  
457 zones at island-wide scales (Ottenwalder, 1999; Borroto-Páez and Mancina,  
458 2011) or animal density estimation (Ottenwalder, 1991; Witmer and Lowney,  
459 2007), and even this research has been limited in terms of taxonomic and  
460 geographic scope and data availability. Out of necessity, we had to use different  
461 field methods and analytical frameworks to investigate spatial ecology in  
462 Hispaniola's two surviving endemic land mammals. However, data from our  
463 multi-year field programme still permit direct comparison of habitat use  
464 between these sympatric species, and challenge previous ecological assumptions  
465 based upon largely anecdotal data from less methodologically rigorous studies,

466 thus revising our understanding about the conservation requirements of these  
467 global-priority mammals.

468 Relatively few studies have estimated home ranges for other small-bodied  
469 tropical mammals, and available studies have employed varying estimation  
470 techniques (e.g. Püttker et al., 2012), making it difficult to assess our Hispaniolan  
471 mammal estimates within wider phylogenetic or ecological contexts. Our hutia  
472 home range estimates are an order of magnitude larger than estimates for  
473 smaller-bodied spiny rats, the closest relatives of capromyids (*Proechimys*  
474 *semispinosus*, 178-2,375m<sup>2</sup>; Endries and Adler, 2005), and are instead  
475 comparable to estimates for other large-bodied cavioid rodents such as agoutis  
476 (*Dasyprocta*, ~10,000-85,000m<sup>2</sup>; Jorge and Peres, 2005) and pacas (*Cuniculus*  
477 *paca*, 14,900-34,400m<sup>2</sup>; Beck-King et al., 1999). Estimates for other large-bodied  
478 terrestrial eulipotyphlans are only available for hedgehogs (*Erinaceus*, ~1,000-  
479 102,500m<sup>2</sup>; Best, 2018); these are extremely variable between different  
480 temperate ecosystems, and difficult to compare with solenodon data. Conversely,  
481 our solenodon estimates are similar to available estimates for Madagascan  
482 greater hedgehog tenrec (*Setifer setosus*, 67,000-137,000m<sup>2</sup>; Levesque et al.,  
483 2012), even though this species is markedly smaller than solenodons (body  
484 mass=200-300g), suggesting that ecologically analogous but phylogenetically  
485 distant insectivorous mammals may have broadly similar spatial requirements  
486 across different tropical regions. Evidence for larger wet season home ranges in  
487 solenodons is consistent with previous observations that solenodon above-  
488 ground activity decreases during the dry season, possibly due to reduced  
489 abundance of invertebrate prey and/or a peak in breeding (Ottenwalder, 1991,  
490 1999). Spatial overlap observed between different solenodon groups tracked

491 within the same season suggests that solenodons do not defend exclusive  
492 territories.

493 The major limiting factor to accuracy in spatial animal behaviour studies is  
494 location error (Horne et al., 2007), and we assessed error associated with both  
495 tracking methods. Our hutia data indicate that target species' behaviour should  
496 be investigated to choose appropriate behavioural scenarios for estimating home  
497 ranges, with GPS tracking in heterogeneous habitats including carefully designed  
498 stationary equipment tests that can be incorporated into analysis. Both  
499 environmental variables and animal behaviour can influence fix precision (Horne  
500 et al., 2007; Recio et al., 2011), and we achieved maximum precision and smallest  
501 estimates in open landscapes, with inclusion of errors from more complex forest  
502 stationary tests increasing estimates through reduced precision (e.g. estimates  
503 increased with the ratio of ground:canopy fixes, due to increased sky availability;  
504 D'Eon et al., 2002; Frair et al., 2004). Calculating unique errors for each fix is  
505 time-consuming and computationally intensive, but error estimates should be  
506 derived for all potential habitats used by target species. Failing to consider  
507 factors affecting fix precision could produce significant differences in home  
508 range estimation for species of conservation concern, with implications for  
509 appropriate management.

510 Most importantly for conservation, home range estimates for Hispaniolan  
511 mammals enabled assessment of habitat use (habitats within home ranges, and  
512 habitat selection relative to available habitats within landscape), providing  
513 important insights into their ability to withstand habitat modification. Previous  
514 studies, not based on systematic assessment of spatial ecology, suggest that both  
515 species are dependent upon undisturbed forest (Sullivan, 1983; Woods and

516 Ottenwalder, 1992; Ottenwalder, 1999), and that hutias might be habitat  
517 generalists that can tolerate greater disturbance than solenodons (Woods, 1981).  
518 However, in mosaic landscapes in the Sierra de Bahoruco, hutias selectively use  
519 forest rather than available modified habitats and are largely restricted to forest  
520 patches. Although variation in precision is considered more likely to affect  
521 estimation of habitat selection (Adams et al., 2013), with home range estimation  
522 relatively robust to GPS measurement error (Frair et al., 2010), only small  
523 changes in hutia habitat composition were seen despite variation in absolute  
524 home range size under different error derivation strategies and behavioural  
525 scenarios. Conversely, solenodons regularly use both forested and modified  
526 habitats, with several individuals detected largely or entirely within pasture and  
527 cropland, and even denning exclusively in these habitats.

528 Data from long-term systematic research therefore contradict assumptions  
529 from older anecdotal data for Hispaniolan mammals, providing a new case study  
530 for the importance of evidence-based conservation. Solenodons are generalist  
531 feeders of invertebrate and small vertebrate prey (Peña Franjul, 1977), and so  
532 may benefit from feeding opportunities in farmed environments (e.g. along field  
533 margins), as seen in other large-bodied eulipotyphlans that are generalist macro-  
534 invertebrate predators (Hof and Bright, 2010), as long as suitable rocky denning  
535 sites are present (Kennerley et al., 2019). The Cuban solenodon has also recently  
536 been reported from forest-agricultural mosaic habitat (Turvey et al., 2017).

537 Conversely, although Hispaniolan hutias are generalist herbivores (Woods and  
538 Ottenwalder, 1992), they are partially arboreal (Sullivan, 1983), and presence of  
539 forest canopy appears to control their landscape-level distribution in the Sierra  
540 de Bahoruco.



541 Our findings suggest it is possible that solenodons might be more widely  
542 distributed across Hispaniola and less rare than previously thought (Verrill,  
543 1907; Allen, 1942; Woods, 1981; Ottenwalder, 1991, 1999), supporting the  
544 proposed Red List downlisting by Turvey et al. (2017). However, habitat loss is  
545 only one threat affecting Hispaniola's biodiversity. We encourage further  
546 research to assess whether native mammal survival and distribution is  
547 controlled by habitat or other environmental parameters (e.g. rocky denning  
548 sites), or by other factors such as presence of invasive mammalian  
549 competitors/predators such as rats, mongooses, free-roaming dogs and feral  
550 pigs (Turvey et al., 2014). Future research should investigate penetration of  
551 invasive mammals into different habitats, and whether presence of native  
552 mammals in modified habitats represents a short-term response to recent  
553 habitat conversion or long-term sustainable persistence (e.g. by documenting  
554 local land-use histories for modified habitats where solenodons occur today).  
555 Our study did not differentiate between different forest types that may further  
556 affect species distribution (e.g. dry forest versus semi-humid forest; new-growth  
557 versus old-growth forest), and it is necessary to determine the level of habitat  
558 modification that Hispaniolan mammals can withstand, and how much forest  
559 needs to remain within agricultural mosaics (cf. Williams et al., 2018). Reported  
560 differences in dependency on forest cover between different solenodon and hutia  
561 populations across Hispaniola might also reflect behavioural flexibility under  
562 different environmental conditions (Woods, 1981), or evolutionary  
563 differentiation, as allopatric populations of both species in northern,  
564 southwestern and southeastern Hispaniola represent distinct subspecies with  
565 diagnostic morphological and genetic differences (Brace et al., 2012; Turvey et

566 al., 2015, 2016). Indeed, Hispaniola is geologically and environmentally  
567 heterogeneous, with a complex diversity of ecosystems across lowland and  
568 montane landscapes that are experiencing differing levels of habitat loss (Lloyd  
569 & León, 2019), making it difficult to generate broad inferences for conservation  
570 planning from a single study landscape. We hope that our new baseline on  
571 Hispaniolan mammal spatial ecology will encourage further rigorous studies of  
572 these enigmatic, unique, and remarkable species, to benefit their long-term  
573 conservation.

574

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582

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752 **Figures**

753

754 **Fig. 1. A**, Map of Hispaniola, showing locations of study sites (1, Mencia; 2, Las  
755 Mercedes). **B, D**, Hispaniola hutias (*Plagiodontia aedium*) with neck collars  
756 carrying GPS units and VHF radio transmitters. **C**, Hispaniolan solenodon  
757 (*Solenodon paradoxus*) with neck collar carrying VHF radio transmitter.

758

759 **Fig. 2.** Hutia 95% KDE home range derived using BBMM under different error  
760 derivation strategies and behaviour scenarios: using basic assessment of  
761 measurement error (unit error), and point error for five scenarios differing in  
762 proportion of time the animal was assumed to spend on ground or in canopy.  
763 Triangle indicates den location.

764

765 **Fig. 3.** Solenodon 95% KDE home ranges in: **A**, Mencia (dry season); **B**, Las  
766 Mercedes (wet season); **C**, Las Mercedes (dry season). Dens used by different  
767 tracked individuals (filled circles) indicated using same colours as individuals'  
768 home ranges. Individuals indicated in yellow and purple are from same group in  
769 **A**; home ranges of different individuals from same group in both **B** and **C** shown  
770 using same colours.

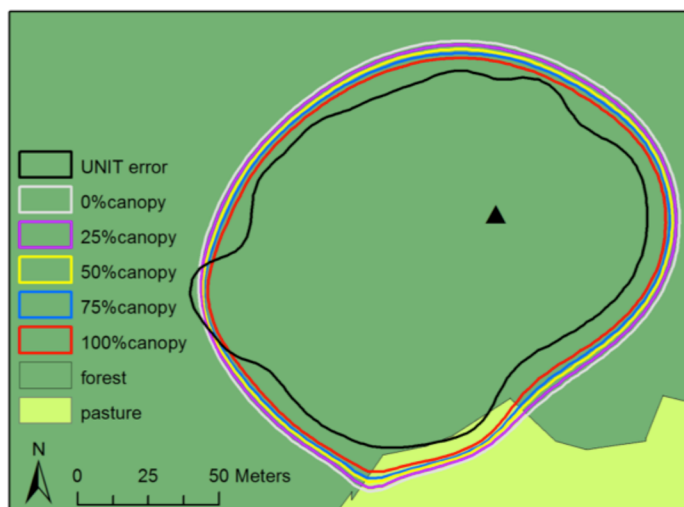
771 **Table 1.** Ranking of models explaining measurement error (ME) and standard  
 772 deviation (SD) in GPS stationary error tests (n=66). ME models ranked using  
 773 Akaike's Information Criterion (AIC); SD models ranked using Akaike's second-  
 774 order corrected Information Criterion (AIC<sub>c</sub>). K=number of parameters;  
 775  $\Delta$ AIC=change in AIC;  $w_i$ =Akaike weight.

776

GPS model description	ME			SD		
	K	$\Delta$ AIC	$w_i$	K	$\Delta$ AIC <sub>c</sub>	$w_i$
Position	4	0	0.43	3	0	0.59
Position+Sky	5	0.17	0.40	4	1.77	0.24
Position+Sky+Position*Sky	6	2.03	0.16	5	3.29	0.11
Sky	4	7.39	0.01	3	5.06	0.05

777





ACCEPTED MANUSCRIPT

