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

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## ABSTRACT

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

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## 1. Introduction

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

The insular Caribbean formerly contained a diverse species-rich assemblage of endemic land mammals, but nearly all of this fauna became extinct during the world’s largest postglacial mammal extinction event, with species losses probably associated with human activities (hunting, landscape transformation, invasive mammal introduction) from the mid-Holocene into the historical period (Cooke et al., 2017). Most of the few surviving species are threatened with extinction (Turvey et al., 2017). Hispaniola, the second-largest Caribbean island (divided politically into the Dominican Republic and Haiti), retains only two non-volant native land mammals, both representatives of endemic Caribbean families: the Hispaniolan solenodon (*Solenodon paradoxus*), a large eulipotyphlan insectivore, and the Hispaniolan hutia (*Plagiodontia aedium*), a large capromyid rodent (Fig. 1). Both species have been considered rare and in danger of extinction, if not already extinct, since the nineteenth century (Cuvier, 1836; Verrill, 1907; Allen, 1942; Fisher and Blomberg, 2011). They are both listed as Endangered by IUCN (2018), and recognised as global conservation priorities based on evolutionary distinctiveness (Collen et al., 2011).

The biology and ecology of Hispaniolan mammals are poorly understood, due to their apparent rarity, secretive nocturnal behaviour, and occurrence in rugged limestone landscapes. Both species have generalist diets, and den in small groups, probably comprising pair-bonded and related individuals including parents and offspring from multiple litters (Sullivan, 1983; Ottenwalder, 1991, 1999; Woods and Ottenwalder, 1992). However, existing data about spatial movements and habitat use are limited, with no information on key parameters such as home range, and such data are only available from studies that usually failed to report survey effort or field methods, or provide analyses or quantitative results.



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

Previous studies focused on investigating native mammal occurrence in different natural vegetation types across Hispaniola. Older studies concluded that both species were associated with broadleaf forest containing rocky crevices for denning, with no indication of differences in habitat selectivity between species (Sullivan, 1983; Woods and Ottenwalder, 1992; Ottenwalder, 1999). Recent country-wide analysis of occurrence inside protected areas suggests that hutias are more dependent than solenodons upon rocky substrate for dens (Kennerley et al., 2019). Ecological inferences about Hispaniolan mammals based on phylogenetic comparisons with related species also provide only limited insights. *Plagiodontia* is the sister taxon to all other living hutias (Fabre et al., 2014), which include both habitat specialists (e.g. mangrove-specialist dwarf hutias *Mesocapromys*) and ecological generalists found across multiple land-cover types (e.g. Desmarest's hutia *Capromys pilorides*), and which exhibit varying levels of obligate arboreal behaviour and restriction to forested environments (e.g. prehensile-tailed hutia *Mysateles prehensilis* versus ground hutias *Geocapromys*) (Clough, 1972; Borroto-Páez and Mancina, 2011). The other surviving solenodon species, the Cuban solenodon (*Atopogale cubana*), is largely restricted to montane and submontane primary forest, although this represents a remnant distribution (Borroto-Páez and Mancina, 2011).

Although ongoing forest loss is occurring across Hispaniola (Pasachnik et al., 2016), native mammal tolerance of habitat modification has not been rigorously investigated. Both species have been reported anecdotally from disturbed secondary forest or partially deforested landscapes, suggesting they might persist at least temporarily under some level of disturbance if suitable rocky crevices are available, and Turvey et al. (2017) recently proposed that both species should be downlisted to Near Threatened by IUCN because there is no evidence of recent subpopulation declines or extirpations. However, populations are considered at high risk of extirpation if disturbance is not reduced and vegetation does not enter successional recovery (Sullivan, 1983; Woods, 1983; Ottenwalder, 1999). The only previous study to consider relative resilience of Hispaniolan mammals to habitat loss was conducted in southwestern Haiti by Woods (1981), who concluded from opportunistic collection records and local reports that hutias were locally more abundant than solenodons in modified landscapes and appeared better-suited to tolerate disturbance, possibly due to more general habitat preferences.

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

## 2. Material and methods

### 2.1. Study sites

Fieldwork was conducted in February 2011–February 2013 near small rural communities in two unprotected landscapes in the southern Sierra de Bahoruco mountains, Pedernales Province, southwestern Dominican Republic: (1) Mencia (18°10'10N, 71°44'25W), elevation = 300–450m; (2) Las Mercedes (18°05'13N, 71°39'55W), elevation = 270–440m (Fig. 1). Rainfall data during the study period from Movebank (Dodge et al., 2013) show that December–March are the driest months. Weather data from Pedernales show little variation in monthly average temperatures (mean monthly high $\pm$ SE = 24.17  $\pm$  1.80 °C; mean monthly low $\pm$ SE = 18.83  $\pm$  1.34 °C) (data from <http://www.worldweatheronline.com/>).

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

All habitats were visited in daytime to locate dens and species-specific signs (Kennerley et al., 2019). Areas where signs were detected were revisited at night. Animals were located by listening for sounds of foraging/movement, and were caught by hand. They were microchipped in the nape using ID-162 FDX-B transponders (1.4  $\times$  8 mm; ZooChip, The Pet Chip Company Ltd, London, UK), and weight, sex, and number of other observed individuals was recorded. No anaesthetics were used. All animal handling/collaring procedures were approved by the Durrell Wildlife Conservation Trust ethics committee.

## 2.2. Spatial behaviour

### 2.2.1. *Hutia*

Animals were studied at Mencia in November 2011–February 2013. An i-gotU GPS Travel & Sports Logger GT-120 (Mobile Action Technology Inc., Taiwan) with modified built-in patch antenna was deployed on each individual using neck collars surrounded with soft tubing. Modifications included: use of Extreme LP1S500 battery (3.7V 500mAh Lithium Polymer); circuit board strengthened using Araldite epoxy; weatherproofing with clear plastic coating (PlastiDip, UK); GPS components rehoused in hard 20 × 46 × 32 mm Camdenboss RX2007/S-5 box (Premier Farnell, UK) with drainage holes. A 23g TW-3 medium mammal tag VHF radio transmitter with whip aerial (Biotrack Ltd., Dorset, UK) was attached to the collar to allow tracking of individuals with a hand-held Yagi 3-element antenna and Sika radio receiver (Biotrack Ltd., Dorset, UK) for welfare monitoring and collar retrieval. Seven units were used. Modified GPS units weighed 35g and the total collar + tag weighed 56g; this is 4.2% of mean adult body mass in the study area (see section 3.1.1), with collars only deployed on individuals where this was <5% of body mass. Units were programmed with a two-night delayed start, to allow animals to habituate to collars and revert to normal behaviour. Units were subsequently scheduled to record fixes (date, time, longitude, latitude, altitude) at 30-min intervals between 9pm and 5am (i.e. excluding periods when animals were in dens), reverting to sleep mode between fixes to extend battery life. Data were stored using built-in memory of 16 Mb. Collars were retrieved after six weeks.

### 2.2.2. *Solenodon*

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

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

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

## 2.3. Home ranges

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

### 2.3.1. *Hutia*

Tracking fixes were screened for outliers by excluding locations for which speeds >2 standard deviations above mean trip speed were necessary between successive fixes (Bjørneraas et al., 2010). Brownian Bridge Movement Models (BBMMs) based on the temporal structure of tracking data were used to calculate home ranges; these enable analysis of data containing temporal autocorrelation, and with GPS error incorporated directly into models to give single values for all points in a track (Horne et al., 2007). Utilisation Distributions (UD; probability density of relocating individuals at any location) for each nightly trip of a *hutia* were produced using the 'BBMM' package in R v3.0.1 (Nielson et al., 2012); these were combined and averaged to produce single UDs for each *hutia* over the tracking period, from which 95% volume contours were calculated (defining areas containing 95% probability of finding individuals; Fieberg, 2007).

Error tests were conducted on stationary GPS units to calculate FSR (number of successful fixes/scheduled fixes) and ME (Euclidean distance between fix position and known reference position, calculated from five location measurements from handheld GPS), with units scheduled to take fixes at 30min intervals over a 24hr period with antennae facing upwards. There was no significant difference in inherent error of ME between units when placed 10 cm above the ground in an open area (mean ± SE = 9.98 ± 8.84m; one-way ANOVA,  $F_{(6,298)} = 0.629$ ,  $p = 0.701$ ); a single unit was used in all subsequent stationary

tests. At three randomly generated forest points within a 150m radius of each hutia study den, error testing was then conducted at both ground-level and canopy-level (mean GPS height in tree  $\pm$  SE =  $8.2 \pm 2.3$ m, range = 4–13m).

The influence of topography and ground/canopy position on ME was modelled using linear mixed models (LMM) with Gaussian error distribution, with stationary test points included as random intercepts to account for non-independence of repeated MEs at each location. Sky availability was calculated for each point at ground and canopy positions in ArcMap (ESRI, 2013) using the Skyline Graph tool and a 30m resolution ASTER Global Digital Elevation Model (DEM) of the Dominican Republic (METI and NASA, 2011). Input variables were scaled to a mean of zero and SD = 0.5. A global model including an interaction term between sky and position, and all possible sub-models, were ranked by Akaike's Information Criterion (AIC); parameter estimates were averaged across all models with  $\Delta$ AIC  $\leq$  6, including zeros as coefficients when variables did not enter particular models (Burnham and Anderson, 2002). Analyses were re-run using the SD of ME at each fix point as the response variable, with models compared using Akaike's second-order corrected Information Criterion (AIC<sub>c</sub>) for small sample sizes.

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

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

### 2.3.2. *Solenodon*

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

Influence of group size (estimated using camera traps and field observations), study site and season (wet/dry) on home range was modelled using LMM with Gaussian error distribution and identity link. Group ID was included as a random term. Input variables were scaled to a mean of zero and SD = 0.5. A global model including only main effects, and all possible sub-models, were ranked by AIC<sub>c</sub>.

## 2.4. *Habitat use*

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

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

## 3. Results

### 3.1. *Fieldwork summary*

#### 3.1.1. *Hutia*

Collars were deployed 18 times, with data retrieved successfully on 12 occasions from 11 individuals (7♂, 4♀) from 11 groups. Deployments contained 20–35 night cycles of data. Group size ranged between 2 and 6 observed individuals

(mean = 3.2). Adult males had a mean body mass of 1322.9g (n = 12, range = 1040–1795g), and adult females had a mean body mass of 1355.0g (n = 5, range = 1180–1530g); total mean body mass for all individuals was 1335.0g (n = 17). GPS data show all study animals used the same dens throughout the survey period.

### 3.1.2. *Solenodon*

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

## 3.2. Home ranges

### 3.2.1. *Hutia*

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

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

### 3.2.2. *Solenodon*

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

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

## 3.3. Habitat use

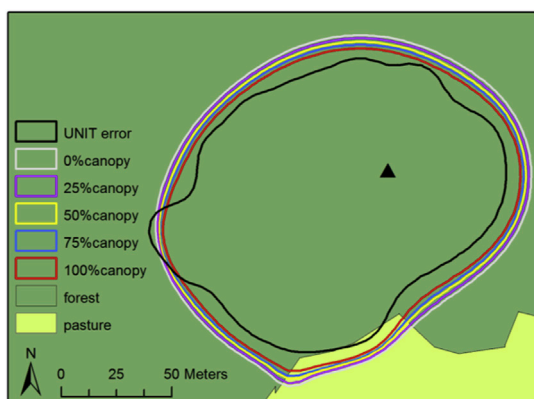
### 3.3.1. *Hutia*

Despite significant differences in predicted home range across strategies and scenarios, there were only relatively small changes in habitat composition within home ranges (Fig. 2; Supporting Information Fig. S2). Hutia were largely restricted to

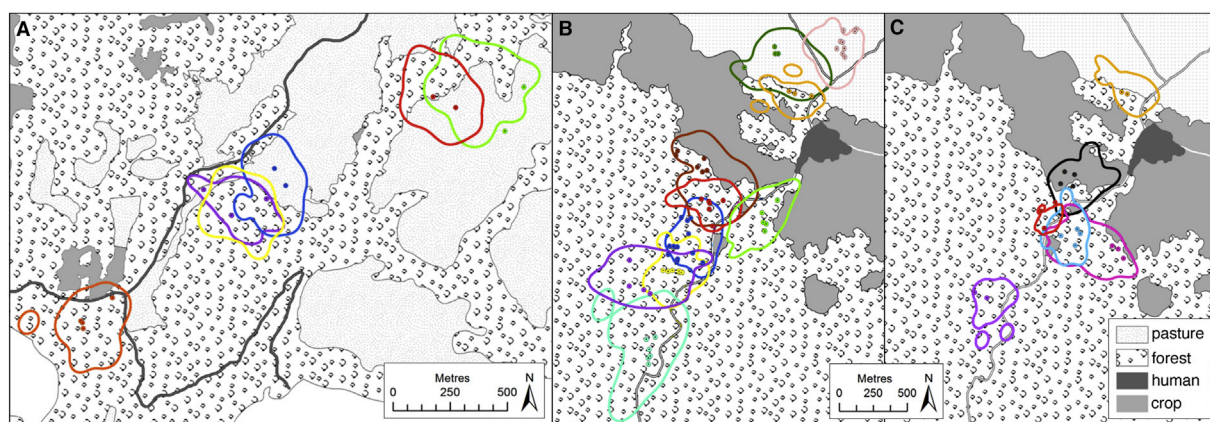
**Table 1**

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

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



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



**Fig. 3.** Solenodon 95% KDE home ranges in: **A**, Mencia (dry season); **B**, Las Mercedes (wet season); **C**, Las Mercedes (dry season). Dens used by different tracked individuals (filled circles) indicated using same colours as individuals' home ranges. Individuals indicated in yellow and purple are from same group in **A**; home ranges of different individuals from same group in both **B** and **C** shown using same colours. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

forest (mean across all strategies/scenarios = 90.3%, strategy/scenario mean range = 88.6–91.5%, total range = 69.1–100%), with limited occurrence in pasture (overall mean = 7.3%, mean range = 6.5–8.3%, total range = 0–30.9%) and minimal occurrence in cropland (overall mean = 1.9%, mean range = 1.5–2.4%, total range = 0–11.6%) or human habitat (overall mean = 0.6%, mean range = 0.5–0.6%, total range = 0–5.1%). All recorded dens were in forest.

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

### 3.3.2. Solenodon

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

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

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

#### 4. Discussion

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

Relatively few studies have estimated home ranges for other small-bodied tropical mammals, and available studies have employed varying estimation techniques (e.g. Püttker et al., 2012), making it difficult to assess our Hispaniolan mammal estimates within wider phylogenetic or ecological contexts. Our hutia home range estimates are an order of magnitude larger than estimates for smaller-bodied spiny rats, the closest relatives of capromyids (*Proechimys semispinosus*, 178–2,375 m<sup>2</sup>; Endries and Adler, 2005), and are instead comparable to estimates for other large-bodied cavioid rodents such as agoutis (*Dasyprocta*, ~10,000–85,000 m<sup>2</sup>; Jorge and Peres, 2005) and pacas (*Cuniculus paca*, 14,900–34,400 m<sup>2</sup>; Beck-Smith et al., 1999). Estimates for other large-bodied terrestrial eulipotyphlans are only available for hedgehogs (*Erinaceus*, ~1,000–102,500 m<sup>2</sup>; Best, 2018); these are extremely variable between different temperate ecosystems, and difficult to compare with solenodon data. Conversely, our solenodon estimates are similar to available estimates for Madagascan greater hedgehog tenrec (*Setifer setosus*, 67,000–137,000 m<sup>2</sup>; Levesque et al., 2012), even though this species is markedly smaller than solenodons (body mass = 200–300g), suggesting that ecologically analogous but phylogenetically distant insectivorous mammals may have broadly similar spatial requirements across different tropical regions. Evidence for larger wet season home ranges in solenodons is consistent with previous observations that solenodon above-ground activity decreases during the dry season, possibly due to reduced abundance of invertebrate prey and/or a peak in breeding (Ottenwalder, 1991, 1999). Spatial overlap observed between different solenodon groups tracked within the same season suggests that solenodons do not defend exclusive territories.

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

Most importantly for conservation, home range estimates for Hispaniolan mammals enabled assessment of habitat use (habitats within home ranges, and habitat selection relative to available habitats within landscape), providing important insights into their ability to withstand habitat modification. Previous studies, not based on systematic assessment of spatial ecology, suggest that both species are dependent upon undisturbed forest (Sullivan, 1983; Woods and Ottenwalder, 1992; Ottenwalder, 1999), and that hutias might be habitat generalists that can tolerate greater disturbance than solenodons (Woods, 1981). However, in mosaic landscapes in the Sierra de Bahoruco, hutias selectively use forest rather than available modified habitats and are largely restricted to forest patches. Although variation in precision is considered more likely to affect estimation of habitat selection (Adams et al., 2013), with home range estimation relatively robust to GPS measurement error (Frair et al., 2010), only small changes in hutia habitat composition were seen despite variation in absolute home range size under different error derivation strategies and behavioural scenarios. Conversely, solenodons regularly use both forested and modified habitats, with several individuals detected largely or entirely within pasture and cropland, and even denning exclusively in these habitats.

Data from long-term systematic research therefore contradict assumptions from older anecdotal data for Hispaniolan mammals, providing a new case study for the importance of evidence-based conservation. Solenodons are generalist feeders of invertebrate and small vertebrate prey (Peña Franjul, 1977), and so may benefit from feeding opportunities in farmed environments (e.g. along field margins), as seen in other large-bodied eulipotyphlans that are generalist macro-invertebrate predators (Hof and Bright, 2010), as long as suitable rocky denning sites are present (Kennerley et al., 2019). The Cuban



solenodon has also recently been reported from forest-agricultural mosaic habitat (Turvey et al., 2017). Conversely, although Hispaniolan hutias are generalist herbivores (Woods and Ottenwalder, 1992), they are partially arboreal (Sullivan, 1983), and presence of forest canopy appears to control their landscape-level distribution in the Sierra de Bahoruco.

Our findings suggest it is possible that solenodons might be more widely distributed across Hispaniola and less rare than previously thought (Verrill, 1907; Allen, 1942; Woods, 1981; Ottenwalder, 1991, 1999), supporting the proposed Red List downlisting by Turvey et al. (2017). However, habitat loss is only one threat affecting Hispaniola's biodiversity. We encourage further research to assess whether native mammal survival and distribution is controlled by habitat or other environmental parameters (e.g. rocky denning sites), or by other factors such as presence of invasive mammalian competitors/predators such as rats, mongooses, free-roaming dogs and feral pigs (Turvey et al., 2014). Future research should investigate penetration of invasive mammals into different habitats, and whether presence of native mammals in modified habitats represents a short-term response to recent habitat conversion or long-term sustainable persistence (e.g. by documenting local land-use histories for modified habitats where solenodons occur today). Our study did not differentiate between different forest types that may further affect species distribution (e.g. dry forest versus semi-humid forest; new-growth versus old-growth forest), and it is necessary to determine the level of habitat modification that Hispaniolan mammals can withstand, and how much forest needs to remain within agricultural mosaics (cf. Williams et al., 2018). Reported differences in dependency on forest cover between different solenodon and hutia populations across Hispaniola might also reflect behavioural flexibility under different environmental conditions (Woods, 1981), or evolutionary differentiation, as allopatric populations of both species in northern, southwestern and southeastern Hispaniola represent distinct subspecies with diagnostic morphological and genetic differences (Brace et al., 2012; Turvey et al., 2015, 2016). Indeed, Hispaniola is geologically and environmentally heterogeneous, with a complex diversity of ecosystems across lowland and montane landscapes that are experiencing differing levels of habitat loss (Lloyd and León, 2019), making it difficult to generate broad inferences for conservation planning from a single study landscape. We hope that our new baseline on Hispaniolan mammal spatial ecology will encourage further rigorous studies of these enigmatic, unique, and remarkable species, to benefit their long-term conservation.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00640>.

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