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RH: Paca home range and habitat selection

Ranging behavior and habitat selection of pacas (*Cuniculus paca*) in central Belize

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Habitat loss and fragmentation present major challenges for wildlife conservation since connectivity between suitable habitat patches is needed for dispersal, allowing for genetic exchange between populations. These exchanges can be particularly important in marginal habitats as they ensure the persistence of populations that are often most vulnerable to natural occurrences or anthropogenic activities. Medium-sized mammals can be particularly susceptible to changes in the landscape and their absence can be an indicator of habitat degradation. In this study, 6 pacas (*Cuniculus paca*), medium-sized mammals that are an important prey of large felids and a popular game species for hunters in Belize, were radio-tracked in the Central Belize Corridor. Home range estimates for these were larger than those documented for pacas inhabiting broadleaf forests of Panama and Costa Rica. When broadleaf habitats were inaccessible due to flooding, pacas selected a savannah habitat with dense vegetation over more open grass savannahs. Knowledge of how pacas and other wildlife use the landscape in the wildlife corridor will allow more effective management by guiding the development of adequate regulations for hunting and resource exploitation.

Key words: corridor, home range, human-influenced, marginal habitat, prey species, telemetry

Habitat degradation and fragmentation threaten wildlife populations globally (Fahrig 2003; Benítez-Malvido and Arroyo-Rodríguez 2008). This is especially apparent in places with high rates of deforestation, such as the neotropics (Fahrig 2003; DeFries et al. 2004) where maintenance of viable wildlife populations often requires connectivity between ever-shrinking forested habitat patches. In the context of connectivity, marginal habitat for a species can be defined as habitat that the species traverses or occupies at low densities between optimal patches. Connectivity is important for wildlife on 2 scales: 1) individuals of wide-ranging species must move through marginal habitat to reach optimal habitat patches, for example jaguars (*Panthera* *onca* Linnaeus, 1758; Rabinowitz and Zeller 2010) and white-lipped peccaries (*Tayassu pecari* Link, 1795; Reyna-Hurtado et al. 2009); whereas 2) species with small ranges and short dispersal distances, such as nine-banded armadillos (*Dasypus novemcinctus* Linnaeus, 1758; Loughry and McDonough 1998), may live at low densities in marginal habitat, depending on partially overlapping home ranges to remain genetically connected with higher-density population centers in areas of optimal habitat. As such, understanding and managing species connectivity depends on knowledge of ranging behavior and use of different habitats. For species with small home ranges and short dispersal distances relative to the scale of habitat fragmentation, connectivity through marginal habitat will become increasingly threatened with the intensification of anthropomorphic pressures on these lands.

The spotted paca (*Cuniculus paca* Linnaeus, 1766), a neotropical, opportunistic, frugivorous caviomorph rodent, hereafter referred to as paca, occurs throughout the neotropics, inhabiting primarily broadleaf forests (Collet 1981; Pérez 1992; Aquino et al. 2009; Goulart et al. 2009). Studies to date, in primary broadleaf forest, suggest that pacas occupy relatively small home ranges (Marcus 1984; Beck–King et al. 1999), and therefore may be vulnerable to the erosion of marginal habitat connecting core populations in forest patches. However, little is known of the ranging behavior or habitat use of pacas outside of primary broadleaf forest. It has been suggested that pacas tend to be more patchily distributed in mosaic landscapes with scattered resources (Marcus 1984; Beck–King et al. 1999; Ulloa et al. 1999).

Pacas are of conservation and management interest throughout their geographic range, as a popular game species for people, an important prey of large carnivores, and as seed dispersers (Dubost and Henry 2006; Aquino et al. 2009; Foster et al. 2016). Population fragmentation and decline of prey species such as pacas may have an impact on human livelihoods and food security (Gordon et al. 2012), shift the competitive balance between co-existing carnivores (Foster et al. 2010a), potentially impact predator survival and exacerbate livestock depredation (e.g. de Azevedo and Murray 2007; Cavalcanti and Gese 2010), and shift the composition of the vegetation within forest systems (Hess 1994; Wright et al. 2000). We investigated the extent to which pacas make use of marginal habitat so that we can better understand the potential for population connectivity, and the associated threats to continued connectivity. This study is the first to document home ranges and habitat selection of pacas outside a state-recognized and established protected area.

MATERIAL AND METHODS

Study area.—The study site was located in the Central Belize Corridor, a human-influenced landscape in Belize, Central America (hereafter ‘CBC’, location 16N 334203E; 191997N UTM NAD27). The CBC is approximately 750 km^2 of low-lying land (≈ 40 m above sea level) comprised of a short grass savannah with shrubs; Caribbean pine (*Pinus caribaea* Morelet) and white oak (*Quercus oleoides* Schltdl. & Cham.) forest; secondary deciduous, moist broadleaf forest; agriculture; and settlements (Goodwin et al. 2011; Doncaster et al. 2012; Kay et al. 2015). Average annual rainfall during the study period (2010 to 2012) was 180 mm, most falling from June to November (wet season), with minimum and maximum temperatures of 21.6 °C and 31.5 °C (National Meteorological Service of Belize). The landscape has a low availability of water during the dry season, and includes seasonally inundated areas during the wet season. The CBC is the last remaining semi-continuous forested landscape connecting the Selva Maya forest block in northern Belize, Guatemala, and Mexico to the forest block of the Maya Mountains in southern Belize. Anthropogenic activities in the CBC include livestock rearing, citrus and sugar cane plantations, slash and burn farms, game hunting, and logging. A 2-lane highway bisects the CBC (Fig. 1).

Trapping and radio telemetry.—Live trapping was conducted between May 2010 and June 2012 (Table 1). Up to 20 live traps (106 x 53 x 40 cm; Tomahawk Live Trap, Hazelhurst, WI, USA) were deployed strategically on trails, with an average distance of 100 m between traps, and baited with fruit. Captured pacas were immobilized using ketamine hydrochloride (48.9 mg/kg) and acepromazine maleate (0.6 mg/kg) and fitted with VHF radio collars (MOD-125, Telonics Inc., Meza AZ, USA). Animal handling and processing was in accordance with the guidelines for the use of wild mammals in research of American Society of Mammalogists (Sikes et al. 2016) and research permits issued by the Government of Belize. Collars functioned for 9 to 12 months, with a weakening and shift in frequency of collar signal near the end of the battery life. Before collar failure, pacas were recaptured to remove the collars.

Telemetry data were collected between June 2010 and July 2012 after the first paca was captured. Collared pacas were located by triangulation (White and Garrott 1990), keeping inter-bearing angles between 20^{o} and 170^{o}. To increase the accuracy in triangulation, azimuths were taken simultaneously by 3 or more observers from different stations, coordinating through 2-way radio contact. Azimuths were recorded at minimum intervals of 5 min for up to a maximum of 5 hours primarily from dusk to dawn, with less frequent tracking during daylight hours when the pacas were more likely at rest. Locations of pacas were estimated by triangulation using program LOAS v4.0.3.8 (Ecological Software Solutions 2013) and calculated with 95% confidence intervals using the maximum likelihood estimator with a X^2 distribution. We discarded locations with error ellipses in excess of 100 ha, and visible outliers.

Home ranges and core areas.—Minimum convex polygons (MCP) were calculated for each paca for comparison with published studies (Table 1). Sequential location data at a minimum of 5-min intervals were used to estimate the mean movement rate per paca and establish the average time to travel along the major axis of the MCP. On average, pacas took 4 hours to traverse their MCPs, and we therefore sampled locations per individual that were ≥ 4 hours apart to ensure independence between points when estimating home range size and determining habitat use.

We established 25 or more independent locations as a reasonable minimum number of points for home-range estimation by kernel analysis considering the time to independence, biological behavior, length of sampling period and the minimum number recommended in the literature (Millspaugh and Marzluff 2001; Moser and Garton 2007). For each paca, 95 % home ranges and 50 % core areas were calculated using a fixed Gaussian (bivariate normal) kernel with least square cross validation as the smoothing parameter in Geospatial Modelling Environment v0.7.2.1 (Beyer 2013). Polygon features were then created for the home ranges and core areas in Arc GIS v10 (ESRI 2010).

Habitat use and selection.—We defined the study area as the combined area of all 95 % kernel areas based on all locations (*n* = 982), including non-independent locations, for all pacas, plus an additional 1-km buffer surrounding this area (based on the maximum linear distance moved by a single paca observed from the data). Habitat types within the study area were identified from satellite imagery and the ecosystem classification map for Belize (Meerman 2011). Two savannah habitats covered 59 % of the study area (savannah with scattered trees, and savannah with dense trees and shrubs), followed by deciduous broadleaf forest on poorly drained terrain (37%), and disturbed habitat, agriculture, and settlements (4%; Table 2). Based on elevation and knowledge of the study area, only 35 % of the broadleaf forest in this area could be considered permanently dry. The broadleaf forest within the study area was damaged by a hurricane in October 2010, and was subsequently burned by forest fires during the dry season of 2011. About 45% of the defined study area burned, including the available broadleaf habitat. The savannah habitat began recovering within a week of the fires but the broadleaf habitat, and particularly its canopy, did not fully recover during the study period.

Habitat use was assessed by compositional analysis (Aebischer et al. 1993) using package adehabitatHS (Calenge 2006) in R (R Development Core Team 2013). Analysis of habitat selection typically involves quantifying use against availability of habitat. Habitat selection and use were assessed at 2 scales: second-order and third-order selection (Johnson 1980). First-order selection concerns the geographical range of the species and was not relevant for our study. Second-order selection refers to the proportion of each habitat in the home range compared to the proportion of each habitat in the study area. Third-order selection refers to the proportion of locations of pacas within each habitat compared with the availability of these habitats within the home range of each paca. Deviations from random habitat use were tested using Wilk's Λ (Aitchison 1982; Aebischer et al. 1993) by comparing the pairwise differences of matching log ratios for habitats and ranked in order of use.

RESULTS

Trapping and radio telemetry.— Six adult pacas (4 males and 2 females) were collared and tracked over a 2-year period, yielding 982 reliable locations. We subsampled these to 267 independent animal locations, mainly in the wet seasons (91%), and the remainder in the early or late dry seasons (9%; Table 1).

Pacas had 95 % kernel home ranges of 68.8 to 212.7 ha ($\bar{X} = 130.6 \pm 51.8$ SD, $n = 6$). Males had 95 % kernel home ranges of 117.6 to 212.7 ha ($\bar{X} = 161.5 \pm 39.3$ SD, $n = 4$), whereas both females had 95 % kernel home ranges of 68.8 ha ($\bar{X} = 68.8 \pm 0$ SD, $n = 2$; Fig. 2). The mean home range of a male was approximately 2.3 times larger than the mean home range of a female ($t = 4.7$, d.f. = 3, $P < 0.05$). Males had core areas (50% kernel area) of 18.1 to 43.2 ha ($\bar{X} = 31.8 \pm 9.0$ SD, $n = 4$) and females had core areas of 10.3 to 13 ha ($\bar{X} = 11.6 \pm 1.4$ SD, $n = 2$). The mean core area of males was 2.7 times larger than that of females ($t = 3.7$, d.f. = 3.4, $P < 0.05$). MCPs of males ranged from 87.5 to 204.9 ha ($\bar{X} = 134.7 \pm 43.1$ SD, $n = 4$) and MCPs of females from 50.7 to 86.7 ha ($\bar{X} = 68.7 \pm 18$ SD, $n = 2$).

Habitat use and selection.—The proportion of habitats within the home ranges of the pacas was a non-random subset of proportions of available habitats in the study area (second order habitat selection randomization test, $\Lambda = 0.0004$, $P < 0.05$). On average, 46 % of the habitat within the home ranges was savannah with dense trees, whereas this habitat type comprised only 15 % of the vegetation cover in the overall study area (Table 2). Thirty-six percent of the habitat in the home ranges was short grass savannah with scattered trees and shrubs; this habitat covered 44 % of the entire study area. Deciduous broadleaf habitat made up 17 % of the habitat within home ranges, yet it covered 37% of the study area. Disturbed habitat only comprised 4% of the study area and was generally avoided (all ranges were ≥ 500 m from disturbed habitat). None of the ranges of pacas in our study spanned the highway; however, during the study a non-collared paca was killed by a vehicle on the highway that traverses the study area**.**

Habitat selection based on locations as the measure of use did not differ from random (third order habitat selection randomization test, $\Lambda = 0.34$, $P > 0.1$). However, repeating this analysis by substituting locations with the habitat composition of core areas suggested possible non-random use (third order habitat selection randomization test, $\Lambda = 0.32$, $P = 0.06$). Together, the second and third order (with core area habitat composition) habitat selection suggest that short grass savannah with dense trees and shrubs was the favored habitat (Table 3).

DISCUSSION

Home range size.—The few studies that have attempted to quantify home range sizes of pacas indicate small ranges within high-density populations in primary broadleaf forest (MCP: Panama, 2.26 ha for $n = 10$ males, 2.36 ha for $n = 12$ females, Marcus 1984; Costa Rica, 3.4 ha for $n = 1$ female, Beck–King et al. 1999). Compared to these published studies of home ranges in optimal habitat, we documented average home ranges in marginal habitat that were 20 and 30 times greater for adult females and ~ 40 to 100 times larger for adult males. Additionally, our study documented range sizes 3 times larger than the only other study that has investigated ranging behavior in marginal habitat (a mosaic agricultural landscape in Colombia) where the monthly home range of a single female was ~19 ha and provided anecdotal evidence that home range size increased with decreased habitat productivity (Ulloa et al. 1999)

The larger home range sizes reported in our study compared to published studies may be attributed to the larger sample size of locations and the longer period of tracking (Beck–King et al. 1999). However, we consider the most likely explanation to be the ecological differences between the sampled habitats. The stable environment of primary broadleaf forests provides environmental conditions in which pacas can satisfy their year-round demands within small areas in close proximity to one another (Dubost and Henry 2006; Maher and Burger 2011). Pacas within our study area most likely needed to travel further in a patchy environment to ensure access to limited resources. Our study shows a substantial increase in home range sizes in habitats with decreased productivity and increased year-round environmental fluctuation, a pattern documented with other caviomorphs (Maher and Burger 2011).

Marcus (1984) found no difference between home range size of male and female pacas inhabiting primary broadleaf forest, whereas in our study in marginal habitat, males ranged farther than females. Marcus (1984) hypothesized a monogamous mating system with pairs of pacas sharing similar-sized ranges. The larger ranges of males compared to females in our study are more consistent with a system in which males might overlap with multiple females. The difference in ranging systems between the 2 study areas might indicate a flexible social structure dependent on density and resource dispersion.

Habitat use and selection.—Second and third order habitat selection by pacas suggested a strong affinity for dense understory and good canopy cover while avoiding flooded forests during the wet season. The 2 savannah habitats in this study differed in the amount of cover they provided and in the drainage patterns of the terrain. The short grass savannah with scattered trees covering almost half of the study area served as a bridge that connected the dense tree and shrub savannah with the broadleaf forest. The broadleaf forest was inundated during the wet season, greatly reducing the availability of dry ground suitable for establishing burrows and potentially restricting the individuals to drier higher areas, as documented in other caviomorphs (Asher et al. 2004; Maher and Burger 2011). Home ranges were established where there was a greater proportion of cover and dry ground, and core areas were centered in dense vegetation, with dense vegetation associations reported in previous studies (Goulart et al. 2009; Harmsen et al. 2010). Although the deciduous broadleaf forest covered a total of 37 % of the study area, only 35 % of this area was dry year round, reducing this habitat type to ~13% total availability within the study area year round. Pacas in our study used 21 % of the available deciduous broadleaf forest indicating selection of this habitat type when available. We hypothesize that selection for residing in the dry short grass savannah with dense trees and shrubs was associated with times when the broadleaf habitat was waterlogged and hence not conducive to habitation. The savannah was drier, potentially providing sufficient cover and more reliable food resources. Overall, the ranging behavior of pacas most likely reflected the patchily distributed resources of dry ground, understory, and canopy cover.

As with other caviomorphs, shifts in ranges of pacas have been recorded in relation to food availability associated with fruiting trees (Marcus 1984; Smythe 1986; Beck–King et al. 1999; Silvius and Fragoso 2003; Jorge and Peres 2005; Aliaga-Rossel et al. 2008; Cid et al. 2013; Emsens et al. 2013). Ulloa et al. (1999) suggested that an increase in ranging area of pacas coincides with the onset of the rains and the fruiting season, as they move in search of food. In our study, the male we tracked for the longest time (7 months) started to shift its range gradually south during the wet season and was last detected in the extreme southern part of its documented range, potentially reacting to changes in fruiting patterns. Assessing the effect of food resources on the movements of pacas was beyond the scope of this study and with only anecdotal information on food availability within the study area, it remains a plausible assumption that food resources was a contributing factor in the southward movement of this paca.

Avoidance of predators or hunters also could influence the decision process during habitat selection by pacas (Lagos et al. 1995; Altendorf et al. 2001; Maher and Burger 2011). Throughout their geographic range, including our study area, pacas are heavily exploited as popular game species for people and are an important part of the diet of large felid species (Foster et al. 2010b, 2016; Figueroa 2013). Pacas avoid open, exposed areas such as wide trails, and reduce activity during bright nights of full moon (Harmsen et al. 2010, 2011). Therefore, a preference for understory canopy, as found in this study, may be an adaptation to avoid predators while active.

Implications for conservation.— Offtake from the wild through game hunting is relatively high when compared to predation-related mortality (Foster et al. 2016). This means that populations of pacas within patchy, marginal habitats (usually close to human settlements) are vulnerable to local extirpation without adequate hunting regulations. Current local regulations are outdated, based on anecdotal information on life cycles, and poorly enforced. Alternatives to hunting such as captive rearing of the species have been explored elsewhere in its range (Smythe 1987, 1991; Govoni and Fielding 2001) and have the potential to greatly reduce the pressure on wild populations in fragmented landscapes. In the fragmented landscape of the CBC, road infrastructure had a very low impact during the study period. Although some of the home range boundaries of our radio-tracked pacas lay within 100 m of the highway, none of the pacas were detected crossing the highway, suggesting a low tolerance for roads. However, a road-killed paca during the study period showed that crossing the highway does happen and contributes to mortality.

Our study suggests that in the absence of optimal habitat, pacas will use marginal habitat, and thus, population connectivity can be maintained in a mosaic landscape lacking contiguous broadleaf forest. Information on the resilience and adaptability of this and other similar species to a changing environment with increasing fragmentation of optimal habitat patches can help guide decisions for their conservation. This study has made a first step in understanding the behavioral ecology of pacas, an important neotropical prey and game species, and seed disperser, under these conditions. We have shown that pacas use marginally suitable habitats within a human-influenced landscape, albeit with larger range sizes than documented in primary forests, which may contribute to their persistence in this region. However, connectivity between these marginal habitats and optimal habitats remains vulnerable within the CBC. Areas of marginal habitat can be vital for the persistence and resilience of paca populations within a wider landscape that is a mosaic of anthropogenically altered habitats. To that end, information presented in our study provides a scientific basis and reasoning for the protection of populations within marginal habitats such those in the CBC. We recognize the need for studies of population density to complement our understanding of movement and habitat use of pacas for the creation of comprehensive regulations for the harvest of the species at a national level, particularly in areas where the species is vulnerable. Conservation action is particularly needed at the regional level, where the paca and other medium-sized mammals can be driven to local extinctions by unregulated hunting and habitat conversion.

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Figure legends

Figure 1.– Study site and corresponding habitat distribution, within the Central Belize Corridor in Belize.

Figure 2.– 95% kernel home ranges and 50% core areas for 6 pacas (*Cuniculus paca*) radio-tracked between June 2010 and July 2012 within the Central Belize Corridor in Belize, projected on the same scale for comparison.

Table 1.– Home range (HR) and core range estimates for 6 adult pacas (*Cuniculus paca*) radio-tracked between June 2010 and July 2012 within the Central Belize Corridor in Belize. *N* (points) corresponds to the subsampled number of independent locations at 4-hour intervals, most of which fall within the wet season.

Animal ID	**Sex**	**MCP (ha)**	**95% Kernel HR (ha)**	**50% Kernel Core (ha)**	***N* (points)**	**Tracked**	**Mass (kg)**
M1	Male	87.5	118	18	42	Jun 2011 - Sep 2011	6.4
M2	Male	125.1	152	31	29	Jun 2011 - Feb 2012	6.8
M3	Male	204.9	213	43	51	Jun 2011 - Feb 2012	7.4
M4	Male	121.1	163	35	69	Jun 2010 - Jan 2011	8.2
F1	Female	50.7	69	13	27	Jun 2010 - Jul 2010	6.2
F2	Female	86.7	69	10	49	Jan 2011 - Aug 2011	6

Table 2.– Percent cover by different habitat types within the study area (combined area covered by 95 % kernel home ranges of all radio-tracked pacas), and mean ± SD (*n* = 6) habitat availability and utilization within entire (95 % kernel) and core (50 % kernel) home ranges.

Habitat	**Coverage in study area (%)**	**Coverage in home range (mean ± SD %)**	**Coverage in 50% Core Area (mean ± SD %)**	**Locations in home range (mean ± SD %)**
Short grass savannah with dense trees and shrubs	15	46.2±14.9	76.1±26.4	71.3±24.9
Short grass savannah with scattered trees	44	36.8±10.5	16.0±10.9	15.3±11.6
Deciduous moist broadleaf forest	37	17.0±13.7	8.1±18.0	13.4±16.9
Disturbed habitat	4	0	0	0

Table 3.– Ranking matrix of the mean pairwise differences of matching log-ratios based on a) comparison of proportional habitat use within the 95% kernel home range with the proportions of available habitat in the study area, and b) comparison of the proportions of telemetry locations with the proportion of each habitat type in the 95% home range. Interpreted by rows only, the rank of order of preference is based on the total number of positive instances per habitat across each row. A triple positive sign indicates a strong deviation from random, suggesting strong selection for the habitat type. A single positive sign indicates a weak selection for the habitat type. A triple negative sign indicates significant avoidance and a single negative indicates weak avoidance.

a) 95% home range versus study area (second-order selection)

	Short grass savannah with dense trees and shrubs	Short grass savannah with scattered trees	Broadleaf	Disturbed	Rank
Short grass savannah with dense trees and shrubs	0	+++	+++	+++	3
Short grass savannah with scattered trees	---	0	+	+++	2
Broadleaf	---	-	0	+++	1
Disturbed	---	---	---	0	0

b) Telemetry locations versus home range (third-order selection)

	Short grass savannah with dense trees and shrub	Short grass savannah with scattered trees	Broadleaf	Rank
Short grass savanna with dense trees and shrubs	0	+++	+	2
Short grass savanna with scattered trees	---	0	-	0
Broadleaf	-	+	0	1

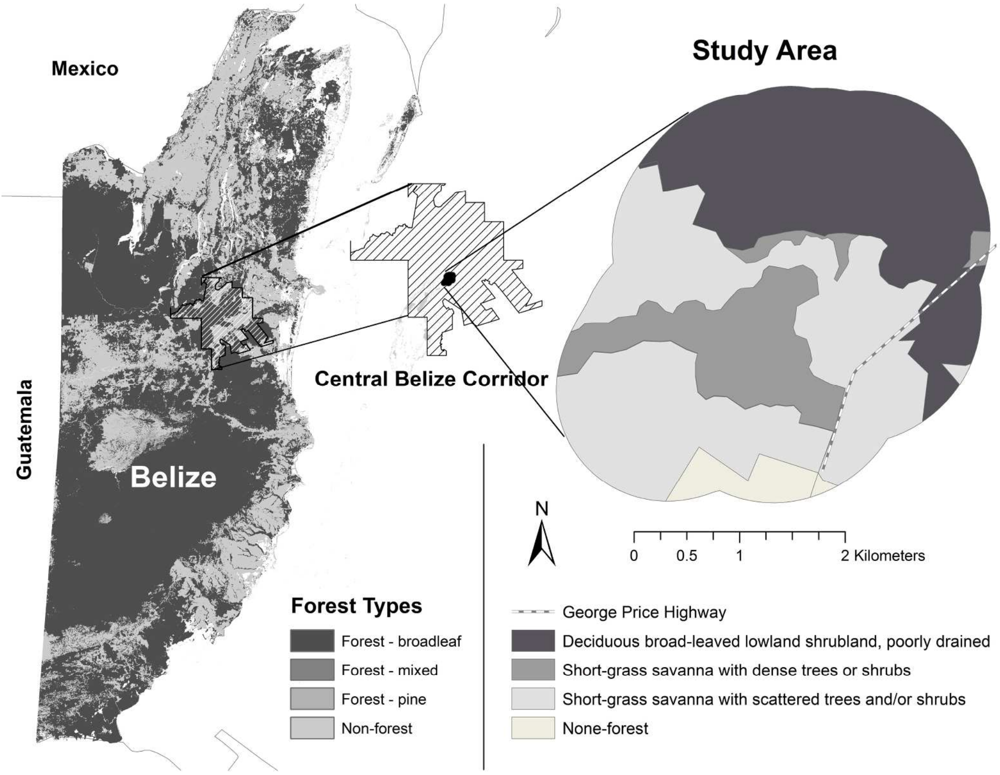

Figure 1.– Study site and corresponding habitat distribution, within the Central Belize Corridor in Belize.

215x166mm (300 x 300 DPI)

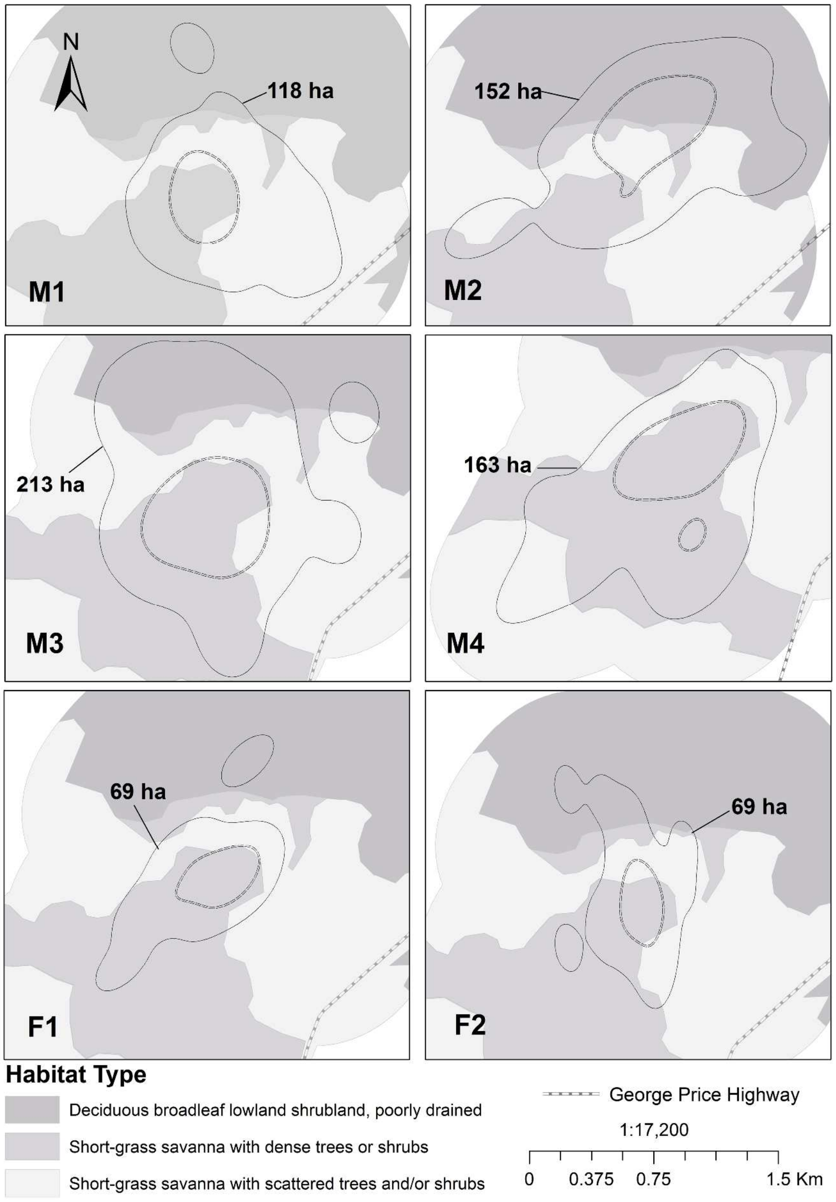

Figure 2.– 95% kernel home ranges and 50% core areas for 6 pacas (Cuniculus paca) radio-tracked between June 2010 and July 2012 within the Central Belize Corridor in Belize, projected on the same scale for comparison.

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