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Habitat use and relative abundance of the Spotted Paca *Cuniculus paca* (Linnaeus, 1766) (Rodentia: Cuniculidae) and the Red-rumped Agouti *Dasyprocta leporina* (Linnaeus, 1758) (Rodentia: Dasyproctidae) in Guatopo National Park, Venezuela

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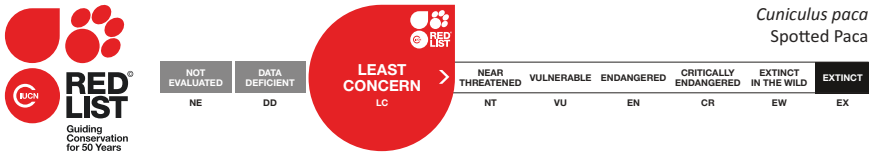
Abstract: The Spotted Paca *Cuniculus paca* and the Red-rumped Agouti *Dasyprocta leporina* are affected by habitat loss and hunting. In Venezuela, their conservation status is unknown, even within protected areas. The objective of this study was to estimate the relative abundance, activity patterns, habitat use, and effect of human activities on these species in Venezuela. To achieve this, 26 camera-trap stations (20.8km^2) were established in Guatopo National Park between February and April 2011, characterization of the habitat was undertaken and occupancy models were created. The relative abundance of the Spotted Paca was 1.62 captures/100trap-nights, with a fully nocturnal activity pattern. The relative abundance of the Red-rumped Agouti was 2.32 captures/100trap-nights, with a pronounced diurnal activity pattern. The occupation probability of the Red-rumped Agouti (0.61 SE 0.02) was higher than that of the Spotted Paca (0.27 SE 0.02). Spotted Pacas were mainly found in areas with mature forest and high tree density, whereas the Red-rumped Agoutis were most frequently found in valleys with little disturbed forest. A positive correlation was found between illegal hunting activities and areas occupied by the Spotted Paca. It is important to strengthen the park control measurements to reduce illegal hunting of Spotted Pacas.

Keywords: Camera traps, *Cuniculus paca*, *Dasyprocta leporina*, habitat use, human activities, illegal hunting, occupancy models, protected area.



Cuniculus paca
Spotted Paca

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INTRODUCTION

The Spotted Paca *Cuniculus paca* (Linnaeus, 1766) and the Red-rumped Agouti *Dasyprocta leporina* (Linnaeus, 1758) are large terrestrial rodents that inhabit a variety of habitats from northern Argentina to southern Mexico (Emmons & Feer 1990; Nowak 1991; Perez 1992). Their diet includes fruits, seeds and nuts (Eisenberg 1989), making them important seed dispersers in the tropics (Forget 1994; Henry 1999). Both species are classified as Least Concern (LC) by the IUCN Red List, mainly because of their wide distribution and occurrence within protected areas (Emmons & Reid 2008; Queirolo et al. 2008).

Both species have a wide distribution in Venezuela and are considered common, however in recent decades they have been negatively affected by habitat loss as well as subsistence and commercial hunting (Silva & Strahl 1994, 1996; Linares 1998). The Spotted Paca is subjected to a high hunting pressure in Venezuela (Images 1–2) because of its high value meat (Silva & Strahl 1994). Its numbers may have declined or it might even have been locally extirpated at some locations where it was previously abundant, as has been reported in other parts of its distribution (Emmons & Feer 1990; Nowak 1991). Nevertheless, neither the Spotted Paca nor the Red-rumped Agouti are considered threatened by the Venezuelan government, and thus they are not protected from hunting (Venezuela 1996a,b) or included in the Venezuelan Red List (Rodríguez & Rojas-Suárez 2008). The conservation status of these rodents is of great concern since no recent studies have been conducted in Venezuela, hence information on their abundance, habitat use, and threats is limited.

With the purpose of improving this knowledge we conducted a study in Guatopo National Park (GNP) using camera traps and occupancy models. Camera-traps greatly facilitate the study of cryptic mammals in remote areas (Karanth & Kumar 2002; Srbek-Araujo & Garcia Chiarello 2005; Kays & Slauson 2008; Tobler et al. 2008; Rovero et al. 2013) and have, therefore, become one of the most common tools for studying mammals in the Neotropics (Kuroiwa & Ascorra 2002; Polisar et al. 2003; Maffei et al. 2005; Noss et al. 2006; Ríos-Uzeda et al. 2007; Schipper 2007; Blake et al. 2012). Some camera trap studies have reported data on the relative abundance (Maffei et al. 2002; de Souza Martins et al. 2007; Tobler et al. 2008), activity patterns (Blake et al. 2012), and occupation probability (Ahumada et al. 2013; Isasi-Catalá 2013) of the Spotted Paca and the Red-rumped Agouti (Table 1).

Occupancy models are primarily used when studying species that are difficult to detect (MacKenzie et al. 2002; Linkie et al. 2007; Ahumada et al. 2013). From these models one can estimate the detection probability (p) and the probability that a site is occupied (Ψ) by a particular species based on the analysis of their detection/non-detection histories (hi) (MacKenzie et al. 2002; Royle & Nichols 2003; MacKenzie et al. 2006). By combining this data with environmental variables from the study area, habitat use can be evaluated (MacKenzie et al. 2002; Royle & Nichols 2003; MacKenzie et al. 2006).

The objective of this study was to estimate the relative abundance, activity patterns, habitat use, and effect of human activities on the Spotted Paca and Red-rumped Agouti in a protected area of the Cordillera de la Costa to assess the conservation status of these species in Venezuela. To do so we conducted a camera trap survey in Guatopo National Park (GNP), where previous studies have reported several cases of illegal hunting of the Spotted Paca (Silva & Strahl 1996; Isasi-Catalá 2012).

MATERIAL AND METHODS

Study area and data collection

GNP (1,224.64km^2, Fig. 1), is located in the Cordillera de la Costa in northern Venezuela (10.03N & 66.41W) (Venezuela 1958). The park is intersected by numerous rivers and mountain ranges with steep inclines and elevations ranging from 200 to 1,430 m (Yerena 1985; MARNR 1992). The climate is warm and humid with an annual rainfall between 1,400–2,800 mm and an average annual temperature between 18–32°C

Abbreviations: AICc - Adjusted Akaike Information Criteria; LV - Amount of leaves in decomposition; Bψ - Beta coefficient for occupancy variables; Bp - Beta coefficient for detection variables; p - Detection probability; hi - Detection/non-detection histories; DP - Detection of predators; DLP - Detection of the two largest predators; WA - Distance to the closest water source; DR - Distance to the main road; HA - Frequency of human activity; FT - Forest type; GNP - Guatopo National Park; GV - Ground vegetation coverage; HV - Horizontal vegetation coverage; IUCN - International Union for Conservation of Nature; LC - Least Concern; c - Model fit; wi - Model weight; δ - Number of parameters; t-n - Number of trap-nights; C - Percentage of activity crepuscular; D - Percentage of activity diurnal; N - Percentage of activity nocturnal; Ψ - Probability that a site is occupied; RAbundance - Relative abundance; RaP - Relative abundances of predators; RaLP - Relative abundances of the two largest predators; sign - Significance of the model; RaAgouti - Site specific relative abundance of the Red-rumped Agoutis; RaPaca - Site specific relative abundance of the Spotted Paca; TO – Topography, TD - Tree density; VV - Vertical vegetation coverage.

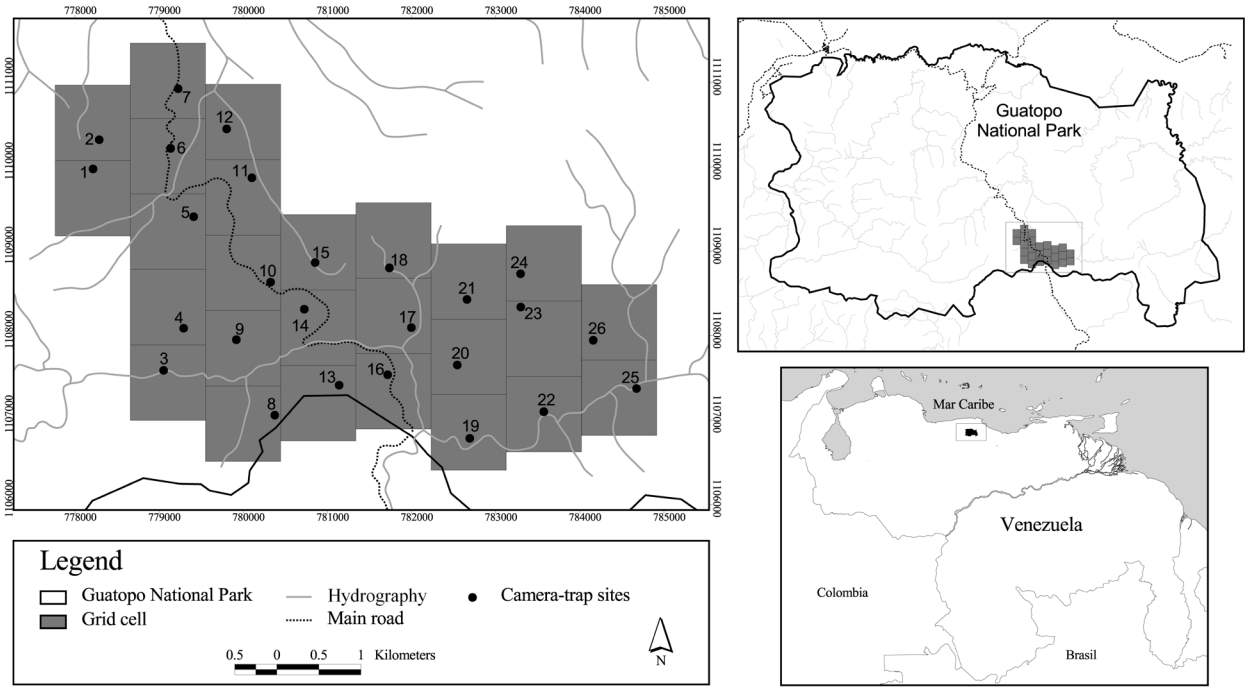

Figure 1. Location of Guatopo National Park in Venezuela and map of the 26 grid cells making up the total study area. Black dots show the location of the detection stations by cameras-traps.

(Castillo & Aponte 2004). Predominant vegetation types within the park are rain forests, cloud forests, and semi deciduous forests (Yerena 1985; Perera-Romero 2006). The national park lies within the most populated regions in the country and is considered vulnerable due to human activities (Castillo & Aponte 2004; Blanco & Yerena 2006).

The study was conducted in the south-western part of GNP (Fig. 1) between February and April 2011. The study area (20.8km^2) was divided into 26 adjacent grid cells (Fig. 1), each containing a photo-capture station: a single camera-trap (Bushnell Trophy Cam, Moultrie Game Spy i65, or Moultrie Game Spy I-40) and an attractor (perfume Chanel N°5, Perfume Factory). Photo-capture stations were established on tracks or other sites where signs of wildlife activity were observed. Two types of data were obtained from camera-traps: count of capture events and detection/no detection of individuals (Karanth & Kumar 2002; MacKenzie et al. 2006; Kays & Slauson 2008). As the Spotted Paca and the Red-rumped Agouti cannot be individually differentiated multiple photos taken within a short period of time might capture the same individual, and so could lead to an overestimation of the abundance of the species. For the count of capture events, photos taken within a 24h period were therefore considered the same event if the photo or video did not clearly show that it was a different individual: male/female, adult/juvenile. This conservative approach follows the methodology used in previous studies (Maffei et al. 2002; González-Maya 2007; Isasi-Catalá 2012).

To assess the rodents habitat use, a characterization of the habitat was conducted in each grid cell according to their area of action (3rd order selection) (Johnson 1980; Dungan et al. 2002; Boyce et al. 2003). At each station, eight environmental variables were determined: ground (GV), horizontal (HV), and vertical vegetation (VV) coverage, amount of leaves in decomposition (LV), tree density (TD), distance to the closest water source (WA), topography (TO), and forest type (FT). GV, HV, and VV was estimated with the program CobCal V.1.0© (Ferrari et al. 2009) based on photographs. LV was measured in cm and TD was calculated according to the Centre Point Square Method (Mostacedo & Fredericksen 2000). WA was categorized as either present within a distance less than 50m, between 50–200 m or greater than 200m from the station, based on the target species estimated dispersal distance (Beck-King et al. 1999). TO was categorized as valley, peak or intermediate and FT was classified as mature or little disturbed forest, based on the classification by Yerena (1985).

Other factors, such as predation (Abramsky et al. 1996; Heithaus & Dill 2002; Sundell et al. 2004), competition (Wasserberg et al. 2006; Head et al.

2012), and human activities (Franklin et al. 2002) might also influence species habitat use. Based on records obtained from camera-traps six additional variables were therefore determined: the relative abundances (RaP) and detection (DP) of predators (P: *Puma concolor, P. onca, Leopardus pardalis*, *L. wiedii,* and *L. tigrinus*), the relative abundances (RaLP) and detection (DLP) of the two largest predators: (LP*: P. concolor, P. onca*), and the site specific relative abundance of each target species (RaAgouti and RaPaca). Further, to evaluate the impact of human activities evidence of illegal hunting and logging recorded in this and previous studies in GNP (Isasi-Catalá 2009, 2012) were used to calculate the frequency of human activity (HA) for each grid cell. Additionally, distance to the main road (DR) was extracted from maps in ArcView 3.2® (ESRI Inc.*, Redlands, CA)*.

Data analysis

Mean relative abundance and site specific relative abundances were calculated, as the number of photo-captures made per 100 trap-nights, for each species. Site specific relative abundances were also calculated and compared between the species using a Mann-Whitney U test in SPSS20.0© (SPSS Inc., Chicago, IL). The activity pattern for each species was divided per hour and compared with the Morisita-Horn similarity index (Horn 1966) using EstimateS (Colwell 2001). The uniformity of its distribution was then evaluated with the Kolmogorov-Smirnov test in SPSS20.0© (SPSS Inc., Chicago, IL). The activity pattern was classified as diurnal (06:00–17:00), nocturnal (18:00–05:00) or crepuscular (05:00–06:00 and 17:00–18:00) (Van Schaik & Griffiths 1996) for comparison with other studies.

Species habitat use was assessed through occupancy models (MacKenzie et al. 2006), using the program Presence 2.4 (Hines 2006). Detection histories for each species were built from records obtained by camera traps using a binary system with zeros indicating lack of detections and ones indicating detections (MacKenzie et al. 2002; MacKenzie et al. 2006). Ψ was estimated from the variables GV, HV, VV, LV, TD, WA, TO, FT, Ra_paca, Ra_agouti, RaP, RaLP, HA and DR, and p from RaP, DP, RaLP, DLP, Ra_paca, Ra_agouti. Models were selected based on model goodness of fit, adjusted Akaike Information Criteria (AICc), AIC model weight, and the dispersion of the models (MacKenzie et al. 2006; Linkie 2008). The top ranked occupancy models (ΔAICc < 3, MacKenzie et al. 2006) were used to determine Ψ of each species for each grid. Ψ were compared between the species with a Mann-Whitney U test implemented in SPSS20.0© (SPSS Inc., Chicago, IL). The variables included in these models were used to determine the characteristics of the habitat used by each species, based on the beta coefficient (MacKenzie et al. 2006): Bψ for occupancy variables and Bp for detection variables.

RESULTS

Relative Abundance and Activity Patterns

A total of 935 trap-nights were performed, during which there were 14 independent capture events of Spotted Pacas at 6 sites and 18 capture events of Red-rumped Agoutis at 12 sites (Table 1, Video 1). Mean relative abundance was calculated for each species, resulting in 1.62 captures/100trap-nights for the Spotted Paca and 2.32 captures/100trap-nights for the Red-rumped Agouti (Table 1). No significant difference was found between the species site specific relative abundances (Mann-Whitney U = 274.50; Z = -1.37; P = 0.17, n = 52).

All captures of the Spotted Paca were made between 21:00 and 05:00 (nocturnal), whereas all except one capture of the Red-rumped Agouti were made between 06:00 and 17:00 (diurnal, Table 1, Fig. 2). The number of captures was not uniformly distributed over the day for either species (Kolmogorov-Smirnov; Spotted Paca: Z = 3.27; P < 0.01; n = 24; Red-rumped Agouti: Z = 3.06; P < 0.01; n = 24), and no overlap between the activity hours of the two species was observed (Morisita-Horn similarity index = 0%).

Habitat use and impact of human activities

According to occupancy models selected (covering >70% of the total explanation power, Table 2), mean occupation probabilities for the Spotted Paca and the Red-rumped Agouti were 0.27 (SE 0.02) and 0.61 (SE 0.02), respectively. The site specific occupation probability was significantly higher for the Red-rumped Agouti than for the Spotted Paca (Mann-Whitney U = 16.00; Z = -5.91; P < 0.01; n = 52). In GNP, the Spotted Paca was associated with areas with high density of trees ($B\psi_{TD}$ = 0.79, SE = 0.54 Table 2), located at greater distances from the main road ($B\psi_{DR}$ = -0.67, SE = 0.63), and characterized by a high presence of predators (Bp_{DP} > 2.04, SE < 0.94), as well as high abundance of the Red-rumped Agouti ($B\psi_{Ra\_agouti}$ = 0.72, SE = 0.56). Areas with a high probability of being occupied by the Spotted Paca also had high frequency of illegal human activities (Bp_{HA} = 0.77, SE = 0.64 Table 2). Red-rumped Agoutis were strongly associated with little disturbed forest ($B\psi_{FT}$ = -13.26, SE = 7.56, Table 2) and valleys ($B\psi_{TO}$ = -0.98, SE =

Table 1. Summary of number of photo-captures, estimated relative abundance (captures/100trap-nights) and activity patterns (%) reported from this and previous studies on *Cuniculus paca* and *Dasyprocta* sp.

Studies	t-n	Captures	RAbundance (SE)	Activity			Location/ Species
				D	N	C	
Cuniculus paca							
This study	935	14	1.62		100		1
Blake et al. 2012	7222	43	1.60*	1	99		2
	6178	115	1.86*				
de Souza Martins et al. 2007	2838	21	0.74		90	10	3
Gomez et al. 2005	3161	174	5.51*	2	96	2	4
Gonzalez-Maya 2007	1980	18	0.91*	28	72		5
Isasi-Catalá 2012	883	18	1.76 (0.43)	0	100		1
Maffei et al. 2002	698	13	1.86	-	-	-	6
	1248	0	0	-	-	-	7
	4815	0	0	-	-	-	8
Michalski & Norris 2011	2707	128	4.73*	0	87	13	9
Srbek-Araujo & Garcia Chiarello 2005	1849	23	1.24*	-	-	-	10
Tobler et al. 2008	1440	14	0.97	-	-	-	11
	2340	33	1.41	-	-	-	11
***Dasyprocta* sp.**							
This study	935	18	2.32	100	0	0	1, a
Blake et al. 2012	7222	103	1.43*	91	3	6	2, b
	6178	217	3.51*				
de Souza Martins et al. 2007	2838	46	1.62	70	15	15	3, a
Gomez et al. 2005	3161	129	4.08*	72	7	21	4, c
Gonzalez-Maya 2007	1980	76	3.84*	88	3	9	5, c
Isasi-Catalá 2012	883	61	6.41 (2.33)	85	7	8	1, a
Maffei et al. 2002	698	44	6.3	-	-	-	6, d
	1248	0	0	-	-	-	7, d
	4815	14	0.29	-	-	-	8, d
Srbek-Araujo & Garcia Chiarello 2005	1849	71	3.84*	-	-	-	10, a
Tobler et al. 2008	1440	50	3.47	-	-	-	11, c
	2340	48	2.05	-	-	-	11, c

t-n - number of trap-nights; Captures - number of captures; RAbundance - relative abundance; SE - standard error; Activity: percentage of activity diurnal (D), nocturnal (N) and crepuscular (C) based on Van Schaik & Griffiths (1996).
1 - GNP-Venezuela; 2 - Tiputini Biodiversity Station-Ecuador; 3 - Caxiuanu National Forest-Brazil; 4 - Madidi National Park and Natural Area of Integrated Management-Bolivia; 5 - Talamanca-Costa Rica; 6 - Private Reserve San Miguelito-Bolivia; 7 - Kaa-Iya National Park (Ravelo)-Bolivia; 8 - Kaa-Iya National Park (Tucavaca)-Bolivia; 9 - Alta Floresta-Brazil; 10 - Santa Lucia Biological Station-Brazil; 11 - Los Amigos Conservation Concession-Peru.
a - *D. leporina*; b - *D. fuliginosa*; c - *D. punctata*; d - *D. azarae*
* Relative abundance was standardized from the original format to facilitate comparison between studies.

0.84). Sites occupied by the Red-rumped Agouti had a high presence of Spotted Pacas ($Bp_{Ra\_paca} > 0.61$, SE < 0.31) but low abundance of large predators ($B\psi_{RaLP}$ = -0.71, SE = 0.59, Table 2). No correlation was found between species occupancy and the other variables studied (like vegetation cover or distance to watercourses).

DISCUSSION AND CONCLUSION

Relative Abundance and Activity Pattern

Relative abundance is a measure based on sampling effort and differences in methodology therefore makes it problematic to compare results between studies (Srbek-Araujo & Garcia Chiarello 2005; Tobler et al. 2008;

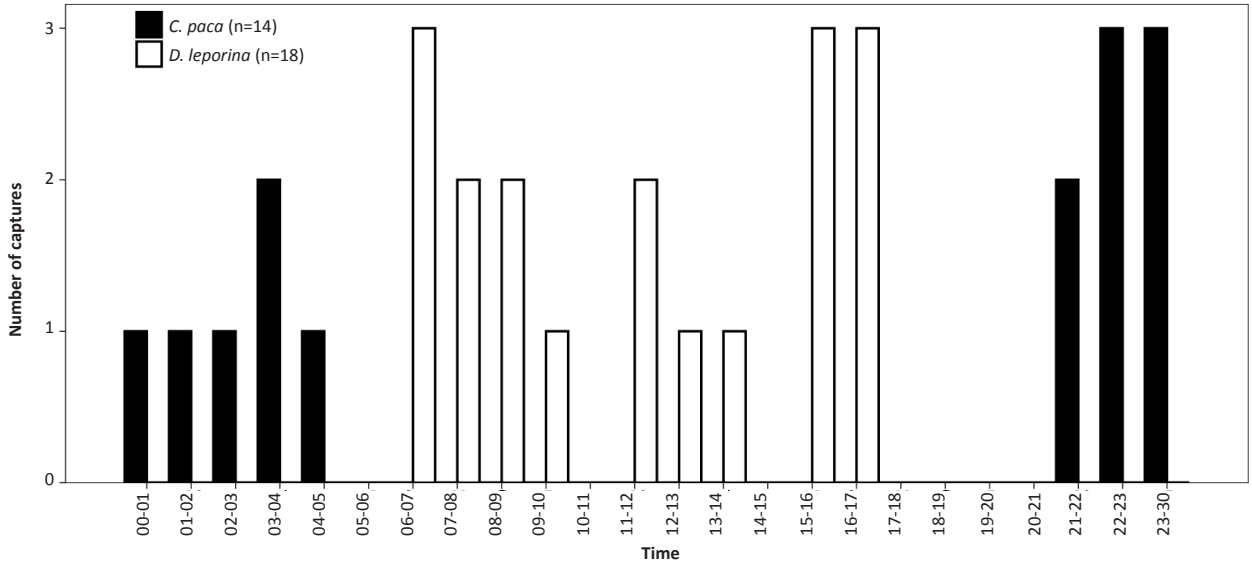

Figure 2. Activity patterns of Spotted Pacas (dark bars) and Red-rumped Agoutis (white bars) in GNP. Spotted Pacas were nocturnal and Red-rumped Agoutis were diurnal (based on Van Schaik y Griffiths 1996), without overlap in their activity.

Table 2. Occupancy models used to evaluate the habitat use of the Spotted Paca and Red-rumped Agouti. Reported models are those contributing to more than 70% of the total explanation of all models for each species.

Occupancy model	ΔAICc	wi	δ	sign	c	Bψ	SE		Bp	SE	
Spotted Pacas											
ψ(.),p(DP)	0.00	0.33	3	0.83	0.55				2.08	0.93	+
ψ(TD),p(DP)	0.94	0.21	4	0.91	0.44	0.79	0.54	+	2.08	0.93	+
ψ(HA),p(DP)	1.78	0.13	4	0.82	0.58	0.77	0.64	+	2.16	0.94	+
ψ(DR),p(DP)	2.27	0.11	4	0.82	0.57	-0.67	0.63	-	2.04	0.92	+
ψ(Ra_agouti),p(DP)	2.84	0.08	4	0.78	0.57	0.72	0.56	+	2.08	0.93	+
		0.85									
Red-rumped Agoutis											
ψ(FT),p(Ra_paca)	0.00	0.38	4	0.79	0.72	-13.26	7.56	-	0.78	0.29	+
ψ(.),p(Ra_paca)	1.74	0.16	3	0.82	0.63				0.67	0.31	+
ψ(TO),p(Ra_paca)	1.98	0.14	4	0.64	0.79	-0.98	0.84	-	0.61	0.31	+
ψ(RaLP),p(Ra_paca)	2.84	0.09	4	0.81	0.72	-0.71	0.59	-	0.70	0.30	+
		0.77									

Ψ - probability of occupation; p - probability of detection; ΔAICc - relative difference in AICc from the top model (ΔAICc); wi - model weight; δ - number of parameters; sign - significance of the model (999 bootstraps) c - model fit; B - beta coefficient for each variable in the models (Bψ - beta for occupancy variable and Bp - beta for detection variable); SE - standard error.
DP - detection/no detection of predators; TD - tree density; HA - frequency of human activity; DR - distance to road; Ra_agouti - relative abundances of *D. leporina;* FT - forest category; Ra_paca - relative abundances of *C. paca;* TO - topography; RaLP - relative abundances of large predators.

Michalski & Norris 2011). Still, it is important to highlight that the relative abundances estimated for both species in our study are within the range reported from previous camera trap studies (Table 1). In a study in Caxiuanu National Forest, Brazil, lower relative abundances were reported for both species (de Souza Martins et al. 2007). In contrast, a higher relative abundance was estimated in Madidi National Park, Bolivia, for the Spotted Paca (Gomez et al. 2005), and in Santa Lucia Biological Station in Brazil (Srbek-Araujo & Garcia Chiarello 2005), as well as in a previous study in GNP (Isasi-Catalá 2012) for the Red-rumped Agouti. In the last two studies the Red-rumped Agouti was one of the mammals with highest relative abundance. Similar relative abundances have been estimated for other species from the genus *Dasyprocta*, such as *D. puntata* in Peru (Tobler et al.

2008) and *D. azarae* in Bolivia (Maffei et al. 2002) (Table 1).

Another variable that has been suggested as appropriate surrogate for evaluating abundance of a species is the occupation probability (MacKenzie & Nichols 2004). In our study, the Red-rumped Agouti had a higher occupation probability than the Spotted Paca. These large rodents have similar characteristics and requirements (Eisenberg 1989; Nowak 1991), thus one could expect to find them in similar abundances. It is possible that hunting pressure on the Spotted Paca has affected its occupation probability. In the 1990s the Spotted Paca was listed as one of the species suffering from the highest hunting pressure in GNP, though during this period these activities were primarily taking place close to the park limit (Silva & Strahl 1994, 1996). Today there is also a significant hunting pressure on the species in the central part of the park, mainly close to the large rivers located in this area (Isasi-Catalá 2012).

The activity patterns obtained in this study coincide with those reported in other studies (Table 1). In Tiputini Biodiversity Station (Blake et al. 2012), Talamanca (González-Maya 2007), Madidi National Park (Gomez et al. 2005) and GNP (Isasi-Catalá 2012) results indicate that the Spotted Paca is nocturnal (Van Schaik & Griffiths 1996), whereas agoutis showed diurnal activity patterns. Ecological factors, such as predation (Sundell et al. 2004), resource availability (Tarnaud 2006), and competition (Wasserberg et al. 2006) can influence the activity pattern of a species. According to a study in Bolivia direct competition between the Spotted Paca and the Central American Agouti (*D. punctata*) is avoided through temporal separation (Gomez et al. 2005). Our results suggest that this is true for the Spotted Paca and the Red-rumped Agouti because we did not find an overlap between the species active hours.

Camera traps have proved efficient tools for studying cryptic medium sized mammals like the Spotted Paca and the Red-rumped Agouti (Srbek-Araujo & Garcia Chiarello 2005). However, to accurately assess the conservation status of these species it is crucial that this sampling method is implemented with designs that give comparable and unbiased population estimators. One of the main limitations of using camera-traps for the study of these rodents is the uncertainty in the identification of independent events. In studies where animals can be differentiated due to individual markings each capture can be included in abundance estimations (Karanth & Kumar 2002; Maffei et al. 2002; Noss et al. 2006; Kays & Slauson 2008; Isasi-Catalá 2012; Negroes et al. 2012). It was, however, not possible to differentiate between individuals neither for the Spotted Paca nor the Red-rumped Agouti (Video 1). Further, both the Spotted Paca and Red-rumped Agouti are territorial species (Linares 1998) and it is therefore likely that captures from the same camera within a short period of time are of the same individual inhabiting that particular territory. We therefore chose to take a more conservative measurement and allow for the possibility that two captures within a 24 hour period might be of the same individual on its daily run. This has been done in earlier studies of species without distinctive markings as well (Maffei et al. 2002; González-Maya 2007; Isasi-Catalá 2012). Some studies have used shorter intervals (even 30 min) to separate events captured with camera-traps (Blake et al. 2012). In total only one capture was eliminated in our study due to this conservative approach.

Habitat use and impact of human activities

In accordance with previous studies (Goulart et al. 2009; Ahumada et al. 2013), the Spotted Paca was mainly found in mature forest with high tree density. The Red-rumped Agouti, on the other hand, was mainly encountered in little disturbed forested areas, which are often contiguous with the mature forest in the park. At present, more than 85% of the park is covered by these types of habitats, with a high variety and abundance of plants that provide food for many species (Isasi-Catalá 2012). High presence of palms in the park could also be a key factor in determining habitat use of the Spotted Paca and Red-rumped Agouti, since it has been reported that their fruits and seeds are an important food source for these species (Emmons & Feer 1990; Ahumada et al. 2013).

Availability of watercourses is probably an important factor for these species, particularly for the Spotted Paca

Video 1. A selection of videos showing events of Spotted Pacas (*Cuniculus paca*) and Red-rumped Agoutis (*Dasyprocta leporina*) taken with camera traps in Guatopo National Park.

Image 1. Spotted Paca (*C. paca*) hunted in Guatopo National Park.

Image 2. Structures used for hunting the Spotted Paca (*C. paca*) in Guatopo National Park.

(Emmons & Feer 1990; Perez 1992; Goulart et al. 2009). However, it is possible that the pattern is not evident at GNP as the park is full of rivers and water ponds (Yerena 1985). Another variable that is often related to the presence of water bodies is topography (Perera-Romero 2006), we therefore expected to find the target species in valleys rather than at peaks, as was the case for the Red-rumped Agouti. Similar results have been reported from another study, indicating that the Red-rumped Agouti has a preference for occupying lowland forest (Ahumada et al. 2013).

Although the Spotted Paca and the Red-rumped Agouti were often separated by space and time, some of the sites with high abundance of one species in GNP were also inhabited by the other species. In La Selva in Costa Rica it has been reported that although the two target species of this study may compete for resources, the Spotted Paca can specialize in fruits whereas the Red-rumped Agouti mainly forages on seeds, thereby decreasing competition for food resources (Ahumada et al. 2013). Both species might however compete with other species for these same resources, such as the Collared Peccary *Pecari tajacu* (Ahumada et al. 2013), which is abundant in GNP (Isasi-Catalá 2012).

The relationship between predators and prey are not always straightforward and might therefore be difficult to interpret. In GNP, sites that were occupied by Spotted Pacas had a high presence of the five predators. In contrast, sites that were occupied by the Red-rumped Agouti were negatively correlated with the abundance of the large predators in the park: jaguar and puma. This might be a result of the predators' choice of prey as well as their activity pattern in the area. Several studies imply that the Spotted Paca is one of the most common prey for large predators, especially jaguars (Aliaga-Rossel et al. 2006; Weckel et al. 2006). A previous study on habitat use of Jaguars in GNP did indicate a high predation pressure by the jaguar also on the Red-rumped Agouti (Isasi-Catalá 2012). This pattern was not observed in the case of Spotted Pacas, and could explain the relationship with predators obtained in our study.

According to the occupancy models, areas occupied by Spotted Pacas had a higher frequency of human activities than areas without any signs of Spotted Pacas. This could indicate that hunters select areas with a high presence of Spotted Pacas in GNP as the species is one of the most sought after due to its commercial value (Silva & Strahl 1994, 1996). Recent signs of a Spotted Paca kill were found during the study in an area where no other observation of Spotted Pacas was made (Images 1–2). The models did not indicate a relationship between human activity and occupation of the Red-rumped Agouti suggesting that this species might be a secondary prey for the poachers in the park. The effect of roads on the occupation of Spotted Pacas in GNP is similar to that reported in the Brazilian Atlantic Forest, where Spotted Pacas were recorded more often on narrow trails than on wider trafficked roads (Goulart et al. 2009). The main road that intersects GNP is associated with major hunting activities within the park (Isasi-Catalá 2012), being the only way for hunters to enter, exit, and transport their prey out of the park.

The occupancy models developed in this study proved to be useful tools for assessing habitat use and occupation probability of the Spotted Paca and the Red-rumped Agouti in GNP. We believe that these models have great potential for studying temporal and spatial patterns of many species, especially those with low detectability, even at large scales. The use of camera trap data in this type of models could be an efficient

method for generating reliable results at low cost in time and effort (Srbek-Araujo & Garcia Chiarello 2005; MacKenzie et al. 2006; Tobler et al. 2008; Ahumada et al. 2013).

Implications for species conservation

As habitat loss and fragmentation have been recognized as threats for the target species of this study (Emmons & Feer 1990; Nowak 1991), the protection of mature and dense forests must be one of the main strategies to ensure the long-term survival of the species. The creation of GNP has indeed resulted in protection and recovery of important forest cover in Cordillera de la Costa (Isasi-Catalá 2012), one of the most threatened habitats in Venezuela (Yerena 1985; Castillo & Aponte 2004). However, it is essential to strengthen the control of human activities that are currently generating loss of forest cover by the park limits (Isasi-Catalá 2012) to ensure the conservation of these species and their habitat. Another great concern for the survival of the target species in GNP is the impact of illegal hunting. A more strict control of who enters the park might be required to reduce the hunting pressure on the Spotted Paca and other game animals within the park.

We believe that it is crucial to increase the information on the status of the Spotted Paca and Red-rumped Agouti in GNP and others areas of Venezuela in order to generate more appropriate conservation guidelines for them. Information gathered in this and future studies should be used to increase the awareness of the general public and policy makers about the current situation and threats to wildlife in the country.

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Resumen: La lapa *Cuniculus paca* y el picure *Dasyprocta leporina* están siendo afectados por la pérdida de hábitat y la cacería. En Venezuela su estado de conservación es incierto, incluso dentro de las áreas protegidas. El objetivo de este estudio fue estimar la abundancia relativa, patrones de actividad, uso de hábitat y efecto de las actividades humanas sobre ambas especies, utilizando modelos de ocupación. Para esto, se establecieron 26 estaciones de cámaras-trampa (20.8km^2) y se realizó una caracterización del hábitat en el Parque Nacional Guatopo entre Febrero y Abril de 2011. La abundancia relativa de la lapa fue de 1.62 registros/100trampas-noche, con un patrón de actividad totalmente nocturno. La abundancia relativa del picure fue de 2.32 registros/100trampas-noche, con un pronunciado patrón de actividad diurno. La probabilidad de ocupación del picure (0.61 EE 0.02) resultó mayor que la de la lapa (0.27 EE 0.02). La lapa se encuentra asociada a áreas de bosque maduros con una alta densidad de árboles, mientras que el picure a bosques ligeramente intervenidos presentes en valles. Las actividades humanas fueron frecuentes en las áreas ocupadas por la lapa. Es necesario mejorar el manejo del parque para reducir la cacería ilegal, principalmente de la lapa.

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Author Contribution: EIC and SMW created the sampling design. EJ, EIC and SMW collected and organized the data. EJ and EIC analyzed the data. EJ, EIC and ARF prepared and reviewed the article.