Research Article

Cavity occupancy by lowland paca (*Cuniculus paca*) in the Lacandon Rainforest, Chiapas, Mexico

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Abstract

Habitat occupancy is a good indicator of wildlife behavior and interactions with their environment. We used camera traps to study the use of cavities by lowland paca (*Cuniculus paca*) in three sites in the Lacandon Rainforest of Chiapas, Mexico. To understand the biotic, environmental, physical, anthropic, and behavioral elements that affect spotted lowland paca, the cameras recorded lowland paca activity in front of 29 cavities. Monitoring occurred continuously in cavities near permanent natural water bodies, underneath roots of trees, or inside hollow logs. These cavities were more frequently found in Montes Azules Biosphere Reserve (MABR), where hunting pressure was low. The daily occupancy and permanence of lowland paca in these cavities were associated with the presence of its offspring. There were no offspring recorded in cavities alongside rivers within grazing areas. This suggests the potential existence of a sink-source type of metapopulation, where community reserves and MABR would serve as source habitat, while riparian corridors would be sink habitat for this species. Lowland pacas used these locations, which were scattered through the study area, so long as hunting was moderate and riparian corridors with safe cavities in large trees were well preserved.

Key words: burrow, use of cavities, time of activity, occurrence

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Introduction

Occurrence and occupancy studies reveal much about wildlife species and their environment. The term "occurrence" refers to the presence or absence of an animal at a given site [1, 2], while "occupancy" refers to the probability or frequency of using a site during a given period of time [3]. A species' occurrence and its occupancy of a site involve the use of resources needed for survival and reproductive success [4]. Terrestrial mammals use cavities as shelters from predators and adverse weather conditions, facilitating thermoregulation, food storage, breeding, resting, and other basic needs [5]. Cavities are used in a discontinuous fashion in relation to time and space [6], mediated by such factors as: biotic (competition, predation, resource availability and breeding season), environmental (weather conditions), physical (protective coverage, closeness to water bodies), anthropic (habitat fragmentation, hunting, closeness to human settlements), or behavioral (parental care, territoriality) [7, 8]. Cavities are therefore vital environmental resources for species that use them since they provide refuge for offspring protection, enabling population growth. One such species is the lowland paca (*Cuniculus paca*), the largest rodent in Mexico [9]. Lowland pacas are solitary and nocturnal, usually spending daytime hours sleeping inside hollow logs, caves, crevices, gaps between rocks, underneath fallen branches and roots, and other kinds of cavities [10]. Each individual normally uses several cavities with one or more entrances, which may be covered with leaf litter to hide them from wild predators or hunters [11, 12]. Its typical habitat is found around water bodies [9]. This rodent is one of the preferred game species throughout the Neotropics because of its tasty meat [13, 14]; it is also an important prey for jaguars (*Panthera onca*), cougars (*Puma concolor*), ocelots (*Leopardus pardalis*) and margays (*Leopardus wiedii*), as well as an active seed predator and dispersal agent [9, 15]. Despite its ecological and nutritional importance for humans, there are only a few studies about the life of lowland pacas in the wild and their use of key resources, such as cavities [12, 14, 16, 17].

Even though this species can tolerate a degree of tropical forest fragmentation [18], its populations have decreased in places where habitat loss and hunting pressure increase [19]. Therefore, studies on its use of basic resources for survival and reproduction (such as cavities) and human impacts on its behavior are needed [20]. The main objectives of our study were: 1) examine the use of cavities and factors (environmental, physical, biotic, anthropic, and behavioral) that influence the occurrence and occupancy of lowland paca in cavities in the Lacandon Rainforest, Chiapas, Mexico; and 2) evaluate the effect of different land uses on the use of cavities by lowland pacas in the study area. We tested the assumption that lowland pacas were present and continuously used cavities with favourable features to avoid predation, and also tested the hypothesis that cavity occupancy in each site with different land use was negatively associated with cavity availability, and positively correlated with the presence of wild predators.

Methods

Study area

Our three study sites were located in the south-eastern sector of Montes Azules Biosphere Reserve (MABR) and in the surrounding localities of Playon de la Gloria and Reforma Agraria, within the Lacandon Rainforest of Chiapas, Mexico (Fig. 1). Montes Azules Biosphere Reserve (3,312 km^2) shelters some of the most diverse and best preserved tropical rainforests in Mexico. The ejidos (communal lands) of Playon de la Gloria (17.4 km^2) and Reforma Agraria (28.8 km^2) are on the edge of the Lacantun River. The main productive activities of residents are agriculture and cattle ranching, as well as fishing, hunting, logging and tourism services [21]. Two different land uses were distinguished in the ejidos. The first ("Anthropic") comprised riparian vegetation corridors and secondary vegetation fragments within a matrix of crops, grazing areas, and human settlements. The second ("Community reserves") were tracts of mature or secondary rainforest surrounded by croplands and pastures. Tourism and research occurred for short periods (*e.g.*, one month) at both community reserves. A third type of "land use" (pristine tropical rainforest) was predominant within MABR. Human presence was scarce at this site (Fig. 1).

Fieldwork

We conducted an intensive search for cavities potentially used by lowland pacas in 15 plots (five plots per site) between April (dry season) and September (wet season) 2013. Each plot was 1,000 m long and 50 m wide. Plots were at least 175 m apart from each other to be considered independent, based on the average home range of lowland pacas [12] (Fig. 1).

The criteria for selecting plots were based on observations of lowland paca tracks and residents' knowledge about the presence of the species at that particular site. Following Aquino et al. [10], the primary criterion for selecting cavities was a minimum diameter of 10 cm and a minimum horizontal depth of 60 cm. Cavities were considered for monitoring if they had an entrance and a clean cavity with fresh footprints and no rubble. Local guides' knowledge about lowland paca presence in certain cavities was taken into consideration. Cavities that were a minimum of 100 m from others were adopted as independent [12], and their physical variables were recorded (Appendix 1).

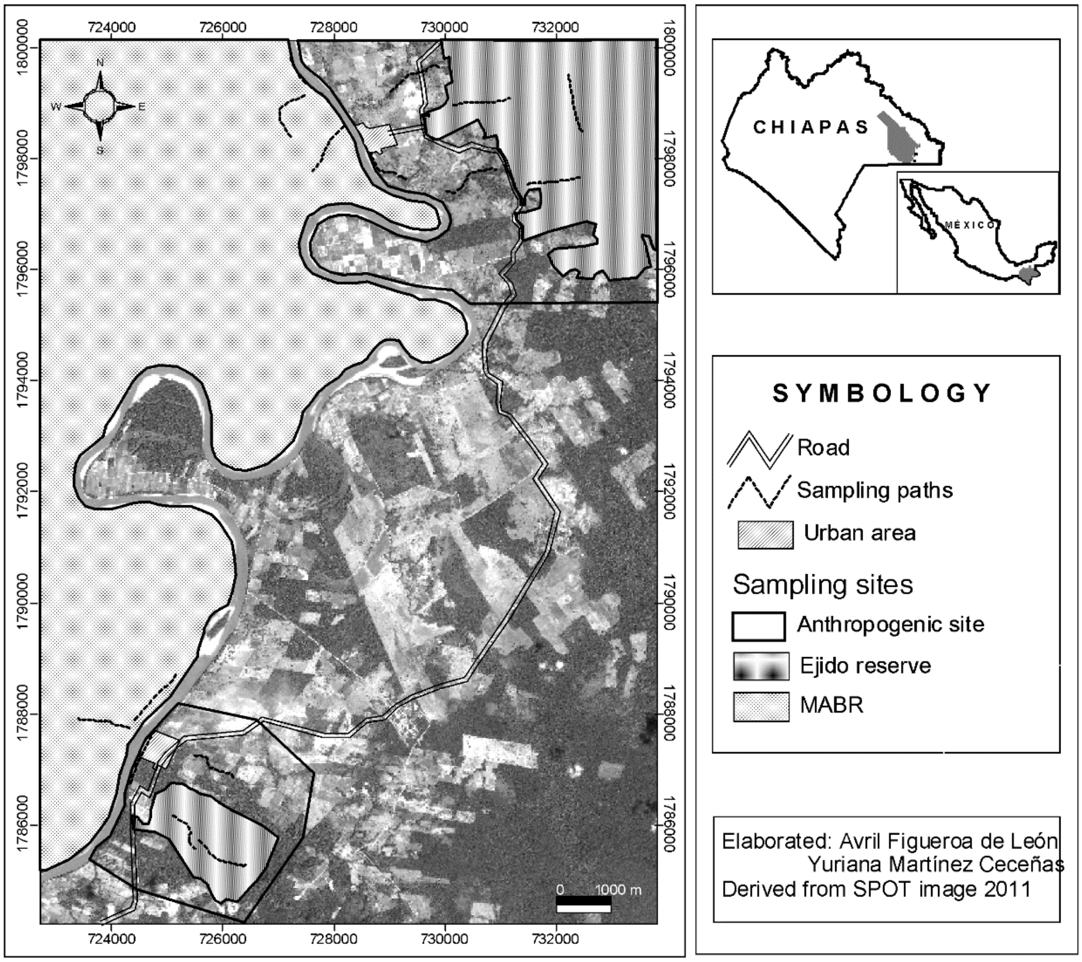

Fig. 1. Study area in Montes Azules Biosphere Reserve, Chiapas, Mexico. The three study sites and plots (sampling paths) walked are shown.

Seasonal cavity occupancy

The frequency of seasonal cavity occupancy was evaluated in four monthly visits (twice per season). We recorded whether each cavity was being used (1) or not (0). The identity of each species using the cavities was verified through camera-trapping, and observing lowland paca individuals inside them on three occasions. Camera-traps (Moultrie D55, Stealth-Cam Q8X and Bushnell Trophy XLT models) were placed in front of cavity entrances with evidence of recent activity (footprints, clean entrance, scratches, and fresh leaf litter covering the cavity). In total, cameras were set in 29 available cavities, of which 16 (dry season) and 19 (wet season) recorded lowland paca activity. Camera-traps were programmed to stay active 24 hours a day. Each camera took three consecutive photographs with 15-second intervals between each shot, or recorded 10 to 30-second videos. The cameras remained in each place for 20 to 40 consecutive days from May 2013 through July 2014.

Daily cavity occupancy

The daily occupancy analysis was carried out by placing camera-traps in front of 16 cavities with lowland paca presence. Six cavities were monitored in the dry season, seven in the wet season, and three in both. Cameras were set in four cavities in the anthropic site, five in the community reserves, and seven in MABR. Video and photographic records identified the species using cavities (including sex and age whenever possible). Some lowland paca adult individuals were identified as follow: 1) The cheeks were more prominent in males than in females; and 2) When there were offspring accompanied by an adult, the adult was always a female. Some of the females could be seen with swollen mammary glands in lactation. Marks, spots, scars and scratches distinguished some individuals as well (Fig. 2).

Fig. 2. Photographs of male (1, 3, 5) and female (2, 4, 6) lowland pacas in the study area. Males were identified by their apparent genitals (3) and by their bulky zygomatic arch (5). Females were distinguished through their apparent mammary glands (6). Examples of individual unique features were battered and opaque fur (1), a missing eye (5), and distinctive spots (2 and 4).

Statistical analysis

To ensure independence of lowland paca records, we verified through camera-trapping that individuals were different among monitored cavities. The database for the dry season was based on the evaluation of 29 cavities, of which two were flooded in the wet season (Table 1). For the monthly occupancy frequency analysis, which was based on the history of cavity use, we obtained the occupancy index for each cavity, incorporating the occupancy probability (Ψ) and the detection probability (p, probability that a lowland paca individual can be recorded, conditional on its presence inside the cavity). For this, we assumed that: 1) every recorded individual and species in the cavities had the same probability of being detected [1, 4]; and 2) the availability of cavities was constant. In order to meet these conditions, we considered the lowland paca population as closed within each season [2]. The analyses were done by the software PRESENCE 6.9 [22], which uses an occupancy index with values from 0 to 1, and provided two levels of cavity use measurements. The first level of use evaluated the occurrence of lowland paca inside the cavities, considering all the > 0 values as lowland paca presence in a cavity, and values of 0 as absences. The second level measured permanence, considered for those cavities with values over 0.75 on the occupancy index. All cavities with values under 0.75 were categorized as occasionally used. Both indices (occurrence and permanence) were considered response variables.

To evaluate factors that influence the frequency of monthly occupancy of cavities, we chose variables that *a priori* might explain the occurrence and permanence of lowland paca in cavities (Appendix 1). These variables were subjected to graphic diagnostics (boxplots and mosaic diagrams) to describe the behavior according to previously described response variables [23]. Generalized linear models (GLM) [24] were built to assess which variables influenced the occurrence and permanence of lowland pacas in cavities (Appendix 1). Due to small sample size, the models were built with up to three variables simultaneously. In all cases, a logistic binominal distribution with logarithm as the link function was adopted. To measure the fit of the models to the data, the Akaike Information Criterion (AIC) and confidence intervals (CI) [23] were utilized. Models with the best adjustment, and where the AIC would show a clear separation as well as having a biological sense, were chosen. The selected models were valued through the weight of the AIC to evaluate the probability of a model being the best, given the data and the chosen models [25]. Model selection was performed with help of the “MuMIn” library [26] included in the "R" software, version 2.0-3 [27].

To analyse the daily cavity occupancy of the lowland paca, only data from 13 cavities where this rodent could be identified individually were utilized. This analysis was based on the frequency of use and the time (counted in days) that it took for a lowland paca to return to the same cavity (called occupancy interval), during 30-day periods. These indices were compared through Kruskal-Wallis’s tests ($P \leq 0.1$) among sites.

Results

Cavity occupancy and associated variables

Lowland paca presence and permanence in cavities were more frequently recorded in MABR during the dry season (Tables 1 and 2).

Table 1. Sample sizes employed on *Cuniculus paca* occurrence and permanence analyses in the Lacandon Rainforest, Chiapas, Mexico. Occupancy indices obtained using the PRESENCE 6.9 program based on the encounter history of lowland pacas in cavities were used to define response variables.

Season	Response variable	0*	1*	n cavities sampled
Dry	Occurrence	10	19	29
	Occupancy frequency	11	18	29
Wet	Occurrence	11	16	27
	Occupancy frequency	15	12	27

0=Cavities without lowland paca (0) and occasional use (values < 0.75); 1=Cavities with lowland paca presence (values > 0) and permanence (values > 0.75).

Table 2. Presence and permanence of *Cuniculus paca* in cavities in the Lacandon Rainforest, Chiapas, Mexico. Numbers represent the percentages of cavities with presence (occupancy index > 0) and permanence (occupancy index > 0.75) by lowland pacas.

Site	Dry season		Wet season	
	Presence	Permanence	Presence	Permanence
Anthropic	62	62	50	17
Community reserve	40	40	40	30
Montes Azules Biosphere Reserve	90	81	82	72

The variables significantly associated with its presence and permanence in cavities were the proximity to permanent water bodies deep enough to dive into, and the type of cavity. Cavities underneath roots and inside hollow trunks were mainly located in MABR (Table 3). These two variables were the only ones included in the best models (validated by AIC weight) that explain the permanence of lowland pacas in cavities during the dry season, while in the wet season, the type of cavity was also included in the best model along with hunting pressure (Table 4). For the wet season, the permanence of lowland pacas in cavities was significantly associated with the type of cavity (Table 3).

Table 3. Variables included in the best generalized linear models (GLM), showing their effect on occurrence and permanence of lowland paca in cavities in the Lacandon Rainforest, Chiapas, Mexico.

Variables in GLM	Dry season		Wet season	
	Occurrence	Permanence	Occurrence	Permanence
	n=29	n=29	n=27	n=27
Closeness to water	Coef.= -2.7 P =0.005	Coef.= -2.2 P=0.01	Coef.= -2.4 P=0.008	
Cavity type	Coef.= 2.3 P= 0.04	Coef.= 2.5 P=0.02	Coef.= 2.6 P=0.02	Coef.= 1.8 P=0.05
Hunting pressure		Coef.= -2.3 P=0.04	Coef.=-2.3 P=0.04	Coef.= -2.2 P=0.02

*Confidence intervals show significant differences.

Table 4. Selection of generalized linear models composed by different sets of variables significantly associated with the presence and permanence of lowland paca in cavities in the Lacandon Rainforest, Chiapas, Mexico.

Analysis	Season	n	Model	Intercept	df	AICc	Weight
Occurrence	Dry	29	Water+cavity type	0.51	4	23.2	0.754
			Water+cavity type+hunting	1.29	5	25.5	0.236
			Water+hunting	3.01	3	31.8	0.01
	Wet	27	Water+cavity type	0.51	4	23.2	0.75
			Water+hunting+ cavity type	1.29	5	25.5	0.23
			Water+hunting	3.01	3	31.8	0.01
Permanence	Dry	29	Water+cavity type	0.63	4	29.7	0.975
			Hunting+potential competitors	3.38	3	37.1	0.025
	Wet	27	Hunting+cavity type	-0.08	4	32.7	0.80
			Cavity+site	-2.04	5	35.5	0.198

Most of the variables (9 out of 12) did not have any significant effect on the occurrence and permanence of lowland pacas in cavities. These variables were: sites with different land use, presence of potential competitors and predators, canopy cover, slope, vegetation type, soil texture and penetrability, distance from cavities to urban areas, roads, and grazing areas. Cavities located underneath roots of living trees had an almost exclusive (90%) presence of lowland paca. On the other hand, underground cavities and those located under fallen logs were utilized both by lowland pacas and by other species such as: striped hog-nosed skunk (*Conepatus semistriatus*), collared peccary (*Pecari tajacu*), northern naked-tailed armadillo (*Cabassous centralis*), nine-banded armadillo (*Dasypus novemcinctus*), four-eyed opossum (*Philander opossum*), Virginia opossum (*Didelphis virginiana*), Central American agouti (*Dasyprocta punctata*), and green iguana (*Iguana iguana*). These species were more frequently observed in the anthropic site, followed by the community reserves, and lastly MABR. The potential predators of lowland paca recorded at the cavities were: ocelot (*Leopardus pardalis), jaguar* (*Panthera onca*), cougar (*Puma concolor*), and tayra (*Eira barbara*)*,* which were present in most of the cavities found in MABR, but were not detected in the anthropic site. Domestic dogs were observed in the community reserve (Fig. 3).

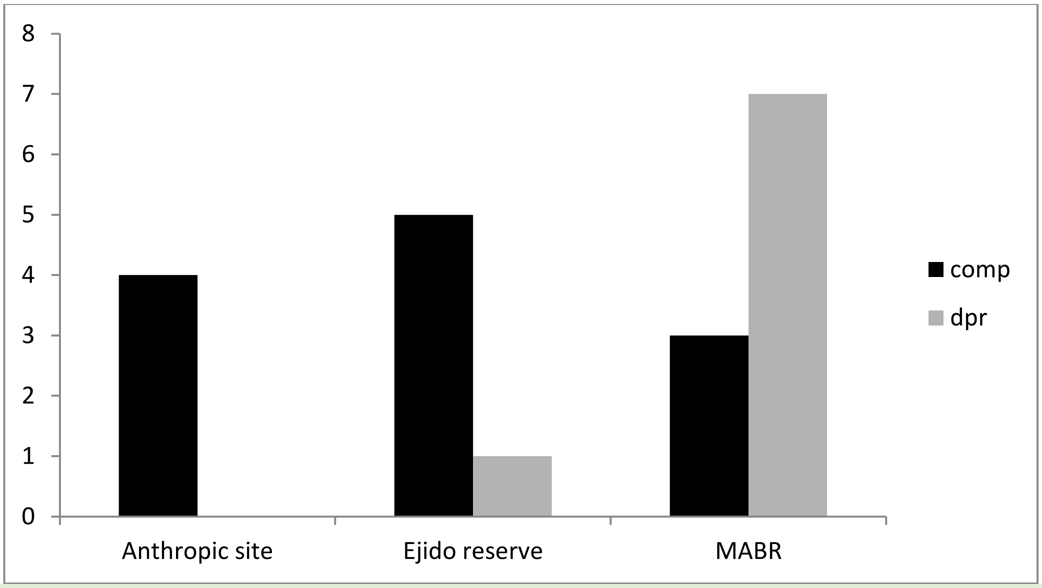

Fig. 3. Records (ordinate) of potential predators (dpr) and competitors (comp) of lowland paca in cavities found in sites with different land use in the Lacandon Rainforest, Chiapas, Mexico.

Through individual identification, 30 different lowland pacas (15 in MABR, 11 in community reserves, and four in the anthropic site) were recorded in 16 monitored cavities, which meant an approximate occupancy rate of two individuals per cavity. A single cavity was occupied by 1-3 individuals, females with offspring being the most frequent, and in the case of a third occupant, this was always a male. Only females were observed hauling dead leaves to cavities and later covering their entrances. In the cavities, seven males, 14 females and nine offspring were recorded. It is noteworthy that the offspring were recorded in the periods April-August and November-December. Females were more frequently found than males in cavities of all study sites. In the anthropic site, there were no offspring recorded and females were recorded in three out of four cavities, while males were found in one out of four cavities. Females and offspring were recorded in the five cavities located in the community reserve, and a single male was detected in one of those cavities. In MABR, females were recorded in six out of seven cavities; males were detected in five and offspring in four (Fig. 4).

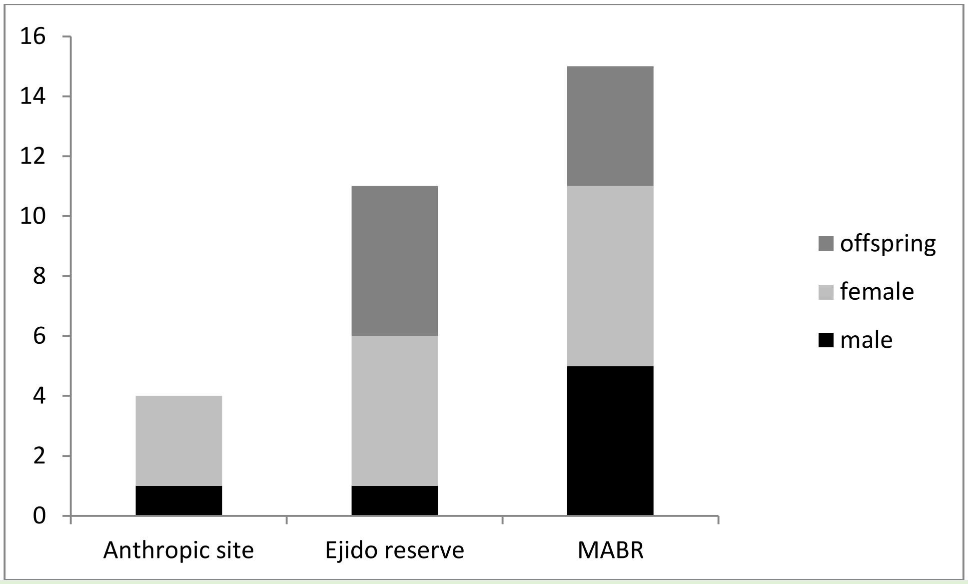

Fig. 4. Numbers (ordinate) of males, females, and offspring of lowland paca observed in cavities at the study sites in the Lacandon Rainforest, Chiapas, Mexico.

The occupancy frequency of cavities was more stable and continuous in the community reserve and MABR than in the anthropic site (x^2=4.1, P=0.1). In the latter, lowland pacas took more days to return to the same cavity (called occupancy interval). In other words, the occupancy of cavities at the anthropic site was more discontinuous and sporadic than in MABR and the community reserve (x^2=4.3, P=0.1; Appendix 2).

Discussion

The presence and permanence of lowland paca inside cavities were more frequently recorded in the dry season, perhaps because in the wet season many of these cavities were underwater for a certain time (from hours to months) and others collapsed, leaving them unusable for lowland pacas, which infers temporary movements of lowland pacas from damaged cavities to others in good condition. The presence of lowland pacas in cavities was less frequent in the community reserve than in the other two sites in both seasons, probably due to high hunting pressure in the community reserve (local authorities reported conflicts caused by hunters invading the reserve from neighbouring communities). In MABR, the permanence of lowland pacas in cavities was recorded in both seasons of the year, possibly because most of the cavities were located under roots and inside hollow logs. The type of cavity was one of the factors that explained the presence and permanence of lowland pacas. All cavities in fallen logs were continuously used in both seasons, perhaps due to their better protection from extreme weather, from the collapse of cavity walls, and from natural predators [28]. Log cavities - being already formed - may also save energy for the lowland paca. The cavities located under thick roots offer multiple entrances and exits for lowland pacas, helping to confuse and deter predators [10].

Another determinant factor for the presence and permanence of lowland pacas in cavities is the proximity to water sources used to escape predators or hunters, as well as meeting a physiological requirement for defecation [14, 17, 28]. Hunting pressure seems to have a direct effect on the occurrence of lowland pacas in the study area and beyond, as observed in previous studies [29]. Some variables that were not significant in our study were considered important for the presence of lowland pacas in other study areas. For example, in Utria Natural National Park, Colombia, the steep terrain was a decisive feature for the presence of cavities used by lowland paca [28], a crucial feature for lowland pacas and other species that use cavities [30, 31]. It has been suggested that the lowland paca is quite tolerant of sites with secondary vegetation and human disturbance [32], which is reflected in the lack of significant effects of land use type, canopy cover, vegetation type, and distances from cavities to human settlements, roads, and grazing areas analysed in our study.

The lowland paca's almost exclusive occupancy of cavities under roots is likely because such cavities are located on slopes along rivers and streams where the lowland pacas can escape from predators by jumping into the water and remaining submerged for several minutes [9]. In addition, the robust jaw of lowland pacas allows them to chew harder seeds than their competitors and to cut thick roots (>15 cm diameter) in their excavations. Cavities inside fallen logs also harbored species such as stripped hog-nosed skunk, collared peccary, northern naked-tailed armadillo, nine-banded armadillo, four-eyed opossum, Virginia opossum, and Central American agouti as well as lowland pacas, perhaps because such cavities were less vulnerable to landslides or looting than those located underground.

Potential competitors of lowland paca were found at 83-100% of the cavities in the anthropic site and the community reserve, likely due to the low availability of cavities, forcing various species to share them. We found that most of the cavities in MABR were under trees and inside hollow logs (diameter at breast height >50 cm) of ceiba tree (*Ceiba pentandra*), breadnut tree (*Brosimum alicastrum*), Sandwith ironwood (*Dialium guianense)*, fig tree (*Ficus* sp.), and bitter angelim tree (*Vatairea lundellii*), which allow lowland pacas to achieve reproductive success and long-term survival. Natural predators such as the jaguar, cougar and ocelot were frequent in MABR but absent from the anthropic site, probably because these species are sensitive to human disturbance.

Female records outnumbered male records in the three study sites and in both seasons, which was corroborated by the sex proportion estimated for the 16 cavities analysed (one male for every two females). This proportion is different from that found in Peru (1:1) for hunted lowland pacas [14]. These differences in sex ratios could be related to the different sources of information between the two studies. The absence of offspring records in the anthropic site cavities may be due to small sample size (n = 4). However, Gallina et al. [32] found that lowland pacas preferred mature forests for breeding, resting and feeding, and used secondary vegetation only to move from one place to another. The presence of lowland paca offspring in the MABR cavities and the community reserve suggests the existence of a potential source-sink metapopulation type in the study area [33], where the anthropic site would be the sink habitat and MABR and the community reserve would be source habitats.

The occupancy frequency was lower in the anthropic site, probably because the distances between cavities were greater when their availability was low, making longer trips for lowland pacas seeking available cavities. This low frequency of cavity occupancy may be due to the absence of offspring inside them. In contrast, offspring were present in all cavities of MABR and the community reserve, associated with parental care of offspring by females. Related to this, we observed in our study area that hauling dead leaves into cavities and later covering their entrances was observed only in female lowland pacas, which conforms with the study by Sabatini et al. [34].

In summary, lowland pacas were present in and continuously used cavities under roots and fallen logs within the study area. Those cavities were located in places with low hunting pressure near permanent water sources, as in the case of MABR. These variables were related to anti-predatory strategies, which supports our first hypothesis. Variables related to habitat disturbance and fragmentation (vegetation type, canopy cover, and land use type) showed no evidence of association with lowland paca occurrence and cavity occupancy. The daily occupancy of cavities by lowland pacas was found to be associated more with behavioural variables such as parental care, than with the presence of predators or the availability of cavities, which implies the rejection of our second hypothesis.

Implications for conservation

Our results suggest that the lowland paca is tolerant of land use change in the Lacandon rainforest as long as riparian corridors, permanent water sources, and large trees providing food and cavities are kept. The availability of cavities with proper conditions for lowland paca survival and reproductive success is an essential requirement to be included in conservation strategies for this species. In our study area, these cavities were primarily found within protected areas with mature tropical rainforest cover, which seem of utmost importance for conserving viable populations of lowland pacas in the long term. Similarly, water sources (*i.e.*, rivers, streams, and ponds) are key elements of lowland paca habitat. Therefore, riparian corridors and live fences between properties must be encouraged and kept to allow lowland paca movements facilitating gene flow between local populations.

However, conservation plans for this mammal should not only preserve source habitat (mature rainforest), but also maintain moderately transformed landscapes constituting sink habitat (*e.g.*, agricultural plots interspersed with small grazing areas and secondary forest fragments). This configuration might favor movements of lowland pacas from mature rainforests to anthropic sites, providing meat and other valuable resources for rural people. Lowland pacas are tolerant of moderate hunting pressure. While heavy hunting usually decimates local lowland paca populations and promotes migration to protected areas, low to moderate hunting may allow lowland pacas to persist in anthropic landscapes at relatively low densities. Avoiding destruction of safe cavities in rocky sites and underneath tree roots may be crucial for the survival of lowland pacas and other wildlife species using the same resource. Conserving lowland pacas and cavities in the territories of rural communities has the additional advantage of providing more prey for hunters and wild predators, thereby reducing the risk of livestock predation and improving the nutrition of poor people through sustainable use.

We recommend studies on the occupancy dynamics of cavities at different spatio-temporal scales. These studies would help to improve our understanding of interactions among species using such cavities and their habitat requirements. If cavities are the primary habitat requirement for lowland pacas and other species, then management actions should be focused on maintaining proper refuges for reproductive success and survival. Shifts in land use alter refuge availability, which in turn affects population dynamics of species using this resource. Thus, further detailed evaluations of variables influencing temporary and permanent cavity occupation by different species are needed for their management and conservation.

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Appendix 1. Variables measured in potential lowland paca cavities in the Lacandon Rainforest, Chiapas, Mexico (2013).

Variable	Unit	Description
Soil penetrability	kg/cm^2	A hand-held penetrometer was used. Values range from 0 to 4.5, with a higher value indicating greater soil resistance and greater hardness.
Slope	%	Measured with a clinometer.
Soil texture	Categories: 1=coarse 2=medium 3=fine	Percentage of sand, silt and clay present in soil. Soil samples (100 g) were collected from each cavity and were analysed at the Soil Laboratory of El Colegio de la Frontera Sur (ECOSUR).
Cavity type	Categories: 1=underground 2=under roots 3=fallen logs	Records based on the structure of the cavity and its form. Type 1: underground > 10 cm); Type 2: underneath thick roots (> 10 cm) of standing trees with DBH > 50 cm; Type 3: inside fallen logs.
Horizontal vegetation cover	%	Measured with a densitometer [35].
Vegetation type surrounding cavity	Categories: 1=mature rainforest 2=secondary vegetation	Vegetation types were grouped into one of the following categories: Type 1: Mature evergreen rainforest dominated by large trees with heights over 25 m; Type 2: Secondary vegetation with trees of up to 25 m high or with predominant bush cover.
Distance to permanent water bodies	Categories: 1= ≤ 87 m 2= > 87 m	Measured in situ using GPS. Category 1: All cavities located at a distance ≤ 87 m from permanent water bodies; Category 2: All cavities at a greater distance. This distance is based on the studies by Beck-King et al. [12], who found that the average home range of a lowland paca is 2.4 ha (a radius of 87 m).

Hunting pressure	Categories: Pressure 1: low Pressure 2: high	Evaluated during the search for cavities, where lowland paca hunting and the destruction of their cavities were considered. A path was considered to have low hunting pressure (1) when hunting was practiced sporadically or less than five times a year (based on information from local people), and to have high hunting pressure (2) when hunting was practiced more than five times a year.
Land use type	Categories: 1: Anthropic 2: Community reserve 3: MABR	The anthropogenic site (1) included croplands, livestock pastures and human settlements in both localities. The second site, located within two communal conservation areas, was surrounded by croplands and pastures, yet at the interior of the two areas there were mature secondary forests (acahuales) and abandoned croplands, as well as mature rainforest. The conservation site (3) was located in the south-eastern sector of Montes Azules Biosphere Reserve (MABR), where mature tropical rainforest was the predominant vegetation type.
Distance to human settlements, roads and grazing areas	m	Linear distance between each cavity and human settlements, roads and grazing areas. Measured on a 2011 Spot image of the study area, only for cavities within the ejidos.

Appendix 2. Frequency of daily use and occupancy interval in sites with different land use in the Lacandon Rainforest, Mexico. Frequencies of use were obtained by dividing the number of days in which lowland pacas visited a cavity within a 30-day period (time in which camera-traps were active). The occupancy interval was the average number of days it took for a lowland paca to return to the same cavity.

Site	n	Frequency of daily use	Occupancy interval
Anthropic	3	3	9.2
Community reserve	3	8	6.7
Montes Azules Biosphere Reserve	7	13	3.7