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ORIGINAL ARTICLE

Gallery forests and open savannas are key habitats for terrestrial mammals in the Colombian Llanos

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Abstract

Habitat conditions are fundamental to provide essential requirements for mammal species to ensure their viability in natural communities. The Colombian Llanos are home to a high mammal biodiversity, but few studies in this region have addressed key aspects of their natural history, such as habitat use and preference. In this study, we evaluated medium and large-size mammal use of gallery forests and open savannas in two locations within the Colombian Llanos, analyzing species' habitat preferences with the hypothesis that mammal species would use and prefer gallery forests over open savannas. We installed 60 camera traps in two sites for 35 days (2100 camera traps / days), covering habitats of both gallery forests and open savannas. Detected species' relative abundances were subjected to Chi-square analysis and Bonferroni 95 % confidence intervals to assess their habitat use and preferences. All recorded mammal species used the gallery forest and ≈ 50 % of these species exclusively used it. Forest preference was high among mammals, but some species found complementary resources in open savannas. Only capybaras revealed a significant preference for the open savanna. We highlight the importance of conserving gallery forests and open savannas in the Colombian Llanos to improve habitat conditions that guarantee mammal survival. Landowners should be encouraged to deploy conservation initiatives to ensure the long-term protection of natural areas required by mammal species.

Keywords: habitat use; habitat preference; camera traps; neotropical mammals; Orinoco basin.

1. Introduction

Savanna ecosystems cover about 43 % of the Earth's land surface [1]. In South America, these ecosystems span an area of 3 000 000 km^2 [2, 3], and Colombia is the country with the third largest extension of natural savannas [4]. Colombian savanna ecosystems primarily occur in the Orinoquia region, which includes the northern part of the eastern plains of Colombia and the western basin of the Orinoco River, accounting for 30.4 % of the national territory [5, 6].

One of the main savanna types is the floodplain savanna, found in the Arauca and Casanare departments, in the eastern part of the country. This region is situated in the northeastern part of the eastern cordillera and along the western boundary of the Orinoco region [1]. The landscapes in these two departments predominantly consist of vast plains, collectively forming an alluvial plain region locally known as the '*Llanos de Arauca–Casanare*' [7]. This region stands out for its remarkable ecosystem diversity, which includes extensive open areas of savannas with grasslands, shrubs, and wetlands, as well as significant forested areas such as gallery forests, *Mauritia flexuosa* palm forests (commonly known as *Morichales*), and Vega forests. All of these habitats are crucial for maintaining species diversity [8].

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Morichales cover vast areas in the Colombian Llanos and represent one pivotal resource for approximately 940 vertebrate species, including 140 mammals [9]. Notably, some studies on mammals have pointed out the importance of gallery forests in the occurrence of different species, especially the rarer ones, as these habitats offer abundant resources for feeding, reproduction, and shelter [10–12]. Moreover, other studies have shown that non-forested open areas, typical of savannas, may not provide sufficient resources for mammals [10]. These areas also pose challenges due to extreme temperature conditions [13] and high predation risk [10, 12]. However, habitat use and preference are context-dependent and vary based on each species' natural history and ecology, many of which remain poorly known in the Colombian floodplain savannas.

Terrestrial mammals play a central role in ecosystem functioning [14–16], as they are fundamental in driving various ecological processes, such as seed dispersal and predation within savanna ecosystems [17]. Even though previous studies have documented significant mammal biodiversity in Colombian floodplain savannas [18–20], our understanding of the spatial niche occupied by terrestrial mammals in this region remains limited. Specifically, there is a notable gap in our knowledge regarding their habitat use patterns and preferences within the highly seasonal floodplain savannas. This knowledge becomes even more critical in regions where extensive landscape transformation plans will be implemented in the coming years. Therefore, understanding mammal habitat use and preference is essential for developing informed conservation policies to prioritize key landscape elements necessary for mammal species persistence [10, 12, 21].

Given the increasing anthropogenic pressures in the *Llanos de Arauca-Casanare* due to economic activities such as oil palm production, livestock ranching, and rice and maize cultivation, among others [22, 23], government institutions need to obtain key information on how species use different habitats within these ecosystems. This information is essential for designing conservation strategies that effectively preserve mammal fauna in this region. In this context, the objective of our study was to evaluate habitat use and preference of terrestrial mammals for open savannas and gallery forests in two locations within the Arauca and Casanare departments. Specifically, we aimed to (1) characterize habitat use based on the relative abundance of mammals in these two types of coverage at each site and (2) analyze mammal habitat preference for gallery forests and open savannas. Our working hypothesis was that mammal species would use and prefer gallery forests over open savannas, as critical resources needed for mammalian survival—such as food, shelter, and protection from predators—are typically more abundant in the former [10–12, 24]. In contrast, we anticipated that mammals would avoid open savannas because of their high predation risk and low structural complexity [10, 12, 24].

2. Materials and methods

2.1. Study area

The study sites encompassed two savanna ecosystems in the departments of Arauca (6.2398°, -71.5863, 172 m, SE-1, **Fig. 1**) and Casanare (5.3204°, -70.8310, 119 m, SE-2, Fig. 1). Local climate exhibits a unimodal rainfall pattern with a short dry period (December to March) and a wet season (from April to November). The two sampling stations of our study are within private natural reserves. Floodplain savannas occur in both sites, and there are different anthropogenic pressures, such as rice crops, oil and gas extraction, and livestock ranching. However, there are differences in the natural composition of the forests and savannas and the extent of anthropogenic pressures at each site [19, 20]. In Arauca, gallery forests are characterized by high tree density and complex stratification, with tree diameters at breast height exceeding 100 cm and canopy

heights up to 25 m [1, 5, 19]. These forests grow on floodplains that receive abundant nutrients from the whitewater Andean rivers (Casanare River) [25, 26]. Conversely, the Casanare region features aeolian savannas where gallery forests are less stratified, with tree diameters at breast height typically less than 50 cm and canopy heights up to 20 m [1, 19].

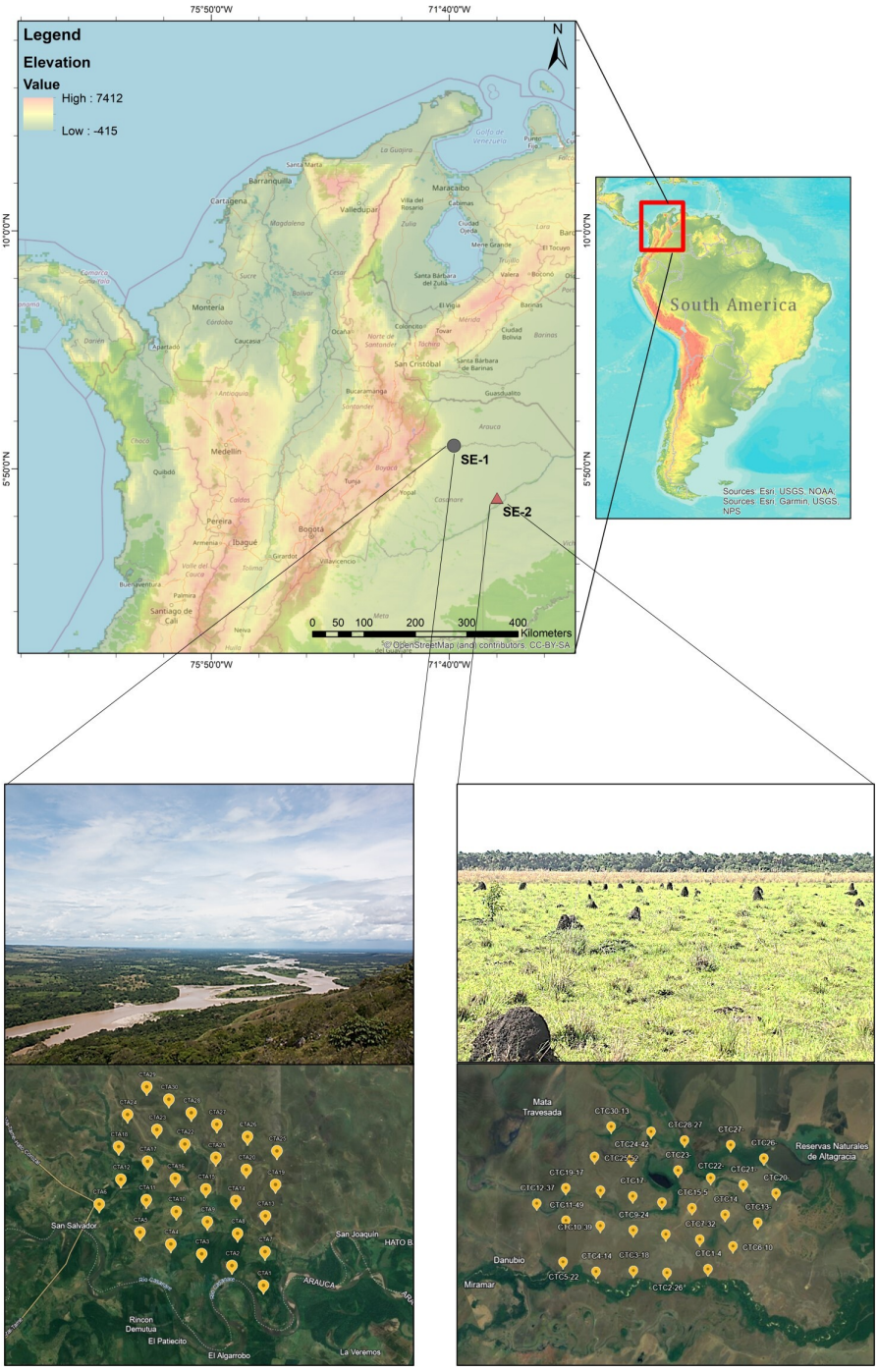

Figure 1. Study sites in the Colombian Llanos. The gray circle represents the floodplain savanna ecosystem in the Arauca department (SE-1), and the pink triangle corresponds to aeolian savannas in the Casanare department (SE-2). The sampling design is illustrated with the placement of camera traps depicted by yellow globes within each sampling site inset, exemplifying the two floodplain savanna ecosystems.

2.2. Study design

This study was conducted between October and November 2017. At each location, 30 points were sampled using a set of 30 camera traps (Bushnell Trophy Cam) placed in the field for 35 consecutive days. Gallery forests and open savannas were adjacent to each other (Fig. 1).

A minimal distance of 1.1 km between camera traps was maintained, effectively covering both gallery forest and savanna habitats with a similar number of cameras depending on landscape configuration within each area (Fig. 1). The total areas covered included 24.6 km^2 in Arauca and 27.06 km^2 in Casanare. In Arauca, gallery forests accounted for 6.68 km^2 (27.15%) of the sampled area, whereas savannas covered 17.92 km^2 (72.85%). In Casanare, gallery forests covered 4.71 km^2 (17.41%) and savannas 22.35 km^2 (82.59%).

Cameras were set at an average height of 20 cm above ground to capture medium- and large-sized mammals (>1 kg) and were programmed to take three pictures per trigger with intervals of one second between pictures. Cameras operated 24 hours, recording the moon phase, date, and picture time. We did not use bait to attract mammals, and to avoid pseudo-replication, we deemed same-species records at a given location independent only if separated by at least one hour [19, 27, 28].

2.3. Habitat use analysis

We defined habitat as an area's resources and conditions supporting an organism's occupancy, survival, and reproduction [29]. Habitat use refers to how an animal utilizes the physical and biological resources within a habitat, whereas habitat preference describes the disproportionate use of given habitats over others [30].

To assess habitat use for each species, we standardized relative abundances (RA) to 100 camera traps / day (*i.e.*, RA = events × 100 camera trap days / sampling effort). When a species occurred in both habitats, we applied a Chi-square test (χ^2) to determine whether there were significant differences in the number of records of that species between the two habitats at each location [31].

We calculated the proportion of records for each species in each habitat, using Bonferroni 95% confidence intervals [32, 33]. The expected values for each habitat were obtained by multiplying the area covered by the number of records observed for each species in that specific habitat. All analyses were made using HaviStat 2.2 [34].

Interpreting the final results of the Bonferroni test involved the following assumptions; (1) If the confidence intervals of the observed value were lower than the expected value, the species avoided that particular habitat. By contrast, (2) if the confidence intervals of the observed value were higher than the expected value, the species preferred that habitat. Finally, (3) when the predicted value fell within the confidence intervals of the observed value, it revealed that the species used habitats proportional to their area [21].

3. Results

After sampling 2100 camera trap / days, we recorded 14 species in Arauca and 12 in Casanare (**Table 1**). Overall, most mammal species were more frequently detected in forests than in open savannas.

Table 1. Medium and large-sized mammal relative abundance estimated by camera trapping scaled 100 camera traps / day.

FAMILY/Species	Common names	Arauca		Casanare	
		Forest	Savanna	Forest	Savanna
CANIDAE					
Cerdocyon thous	Crab-eating fox	0.38	0.57	Not detected	0.29
CAVIIDAE					
Hydrochoerus hydrochaeris	Capybara	0.10	Not detected	0.10	2.38
CERVIDAE					
Odocoileus virginianus cariacou	White-tailed Deer	1.05	2.38	0.38	4.38
Subulo gouazoubira	South American brown brocket	0.57	Not detected	Not detected	Not detected
CUNICULIDAE					
Cuniculus paca	Paca	4.57	Not detected	2.38	Not detected
DASYPROCTIDAE					
Dasyprocta fuliginosa	Black agouti	12.57	Not detected	5.14	Not detected
DASYPODIDAE					
Dasypus novemcinctus	Nine-banded armadillo	2.00	0.10	0.57	Not detected
DIDELPHIDAE					
Didelphis marsupialis	Black-eared opossums	1.71	Not detected	2.67	Not detected
FELIDAE					
Leopardus pardalis	Ocelot	1.24	Not detected	0.57	Not detected
Herpailurus yagouaroundi	Jaguarundi	0.29	Not detected	Not detected	Not detected
Puma concolor	Puma	Not detected	Not detected	0.48	Not detected
MYRMECOPHAGIDAE					
Tamandua tetradactyla	Southern tamandua	2.48	0.29	1.43	0.48
Myrmecophaga tridactyla	Giant anteater	2.76	1.52	0.57	2.10
MUSTELIDAE					
Eira barbara	Tayra	1.33	Not detected	Not detected	Not detected
TAYASSUIDAE					
Dicotyles tajacu	Collared peccary	13.24	Not detected	0.57	0.10

Indeed, eight species were not registered in savannas, including *Cuniculus paca, Dasyprocta fuliginosa, Didelphis marsupialis, Leopardus pardalis, Puma concolor, Herpailurus yagouaroundi, Subulo gouazoubira*, and *Eira barbara*. However, it is worth noting that we consistently detected all these species in gallery forests, at least in one of the study sites (Table 1).

Regarding habitat preference, in Arauca, *Dasypus novemcinctus*, *Myrmecophaga tridactyla*, and *Tamandua tetradactyla* preferred gallery forests over open savannas, while *Cerdocyon thous* and *Odocoileus virginianus cariacou* used both habitats equally (Fig. 1, **Table 2**). In Casanare, *T. tetradactyla* and *Dicotyles tajacu* preferred gallery forests, whereas *Hydrochaerus hydrochaeris* preferred open savannas, and *M. tridactyla* and *O. virginianus cariacou* used both habitats in the same proportion (**Fig. 2**, Table 2).

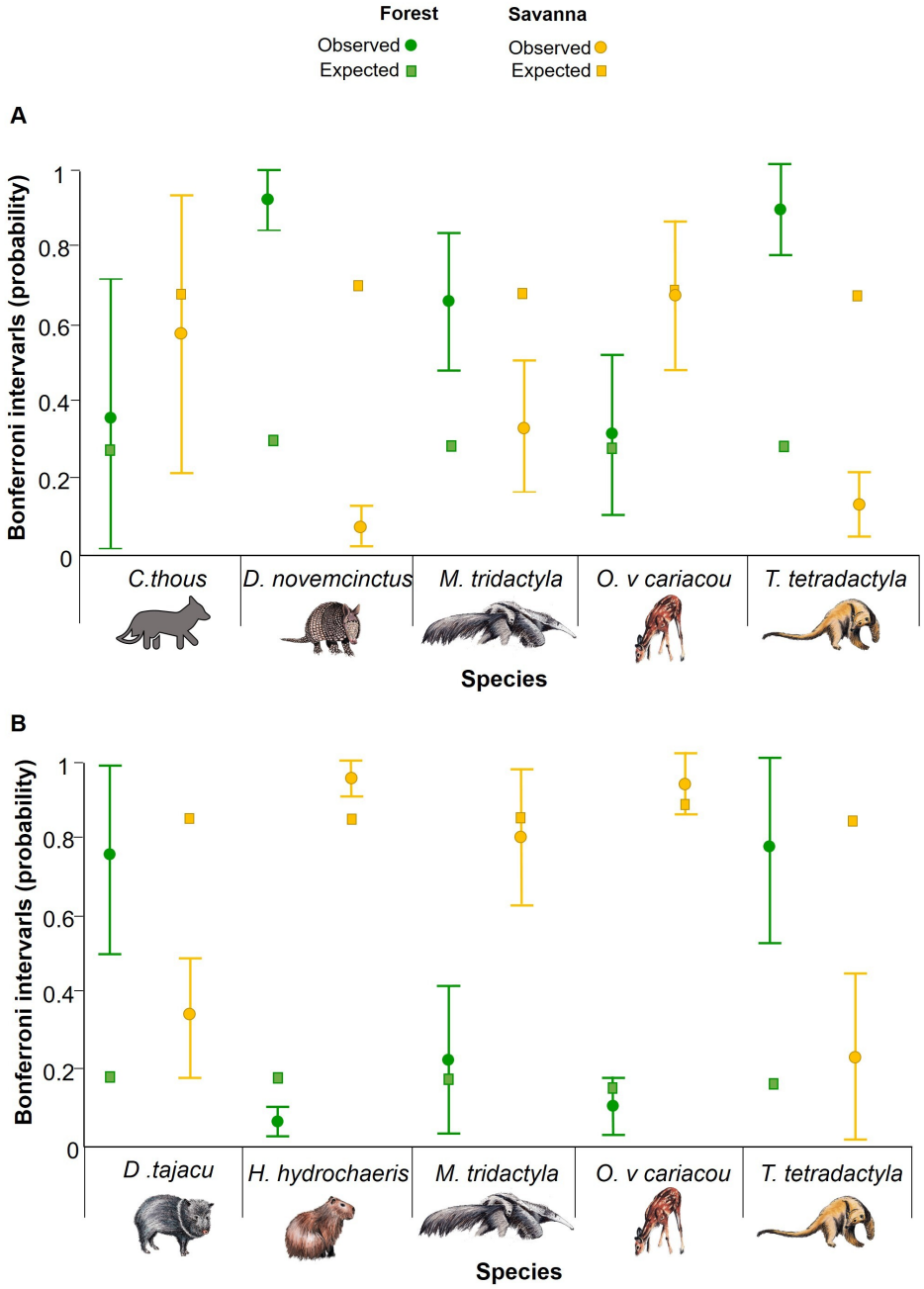

Figure 2. Bonferroni 95 % confidence intervals of five mammal species in forest (green) and savanna habitats (yellow) from savanna floodplains ecosystems of **(A)** Arauca and **(B)** Casanare departments in Colombia. Squares represent expected use values and circles observed values. Habitat use: when the expected value fell within the observed confidence intervals. Habitat preference: when the confidence intervals of observed value were higher than expected value. Habitat avoidance: when the confidence intervals of the observed value were lower than the expected value.

Table 2. Chi square (χ^2) values of medium and large-sized mammals present in two habitats within each surveyed site. Significant values (P < 0.05) in habitat preference are represented in **bold**. No significant difference indicates that species utilize both habitats equally, showing no particular preference.

Species	Arauca			Casanare		
	χ^2	Std. error	P value	χ^2	Std. error	P value
Cerdocyon thous	0.771	0.057	0.361	-	-	-
Dasypus novemcinctus	47.25	0.011	**<0.001**	-	-	-
Myrmecophaga tridactyla	27.175	0.012	**<0.001**	0.298	0.016	0.574
Odocoileus virginianus cariacou	0.205	0.015	0.646	3.703	0.006	0.079
Tamandua tetradactyla	50.399	0.012	**<0.001**	34.424	0.024	**<0.001**
Dicotyles tajacu	-	-	-	15.621	0.055	**<0.001**
Hydrochoerus hydrochaeris	-	-	-	4.581	0.008	**0.0323**

4. Discussion

Our observations partially supported this investigation's leading hypothesis, as habitat use and preference results highlight the importance of conserving gallery forests and open savannas for medium and large-sized mammals in the Colombian Llanos. Notably, given that all species always used forests to some extent, at least in one of the sites, and, more importantly, half of them were exclusively found in this habitat, gallery forests are a critical conservation priority for the survival of mammal species (Table 1).

Specialist carnivores such as *P. concolor*, *H. yagouaroundi*, *L. pardalis*, and *E. barbara* depend on high-quality habitats that provide specific resources, including water bodies, adequate escape cover, and shelter trees that enhance refuge conditions [10, 35–37]. In particular, large felids such as *P. concolor* tend to avoid open pastures and agricultural matrices, strongly associating with forested areas, edges, or densely vegetated habitats that offer abundant prey [12, 38]. Many of these prey species were observed in gallery forests during this study (*e.g.*, *S. gouazoubira*, *H. hydrochaeris*, *O. virginianus cariacou*, *D. tajacu*).

Gallery forests also provide suitable soil conditions for key ecosystem engineers like *D. novemcinctus*, as this species directly relies on soil quality for digging burrows used for feeding, hiding from predators, thermoregulation, and raising young [39, 40]. Studies in the agricultural landscapes of the Brazilian Cerrado have shown that native forest cover and proximity to watercourses significantly influence the occupancy of *D. novemcinctus* [11]. Additionally, the strong preference of armadillos for gallery forests over open savannas may offer adequate daytime cover to rest and avoid exposure to aerial and terrestrial predators [41].

Other insectivorous mammals, such as *T. tetradactyla*, specialize in arboreal ants from the *Camponotus* and *Cephalotes* genera, which are primarily found in forested areas [42,43]. Similarly, frugivorous mammals like *D. tajacu* can form large groups of up to 20 individuals and, despite their ecological plasticity to inhabit both forests and agricultural areas [44], they heavily rely on fruits, seeds, nuts, and roots [45–47]. These resources are more abundant in forested environments where various palm species offer substantial quantities of these resources.

However, our findings demonstrate that different mammal species also use natural open savannas, and some of these mammals can meet their requirements by utilizing savanna and forest habitats. Notably, *H. hydrochaeris* was the only species that preferred open savannas over gallery forests. Although capybaras generally prefer shaded areas with trees and shrubs for resting, they can also use the shelter provided by pastures within an open savanna [48, 49].

More generalist species, like *C. thous*, have been recorded in highly transformed landscapes, including oil palm plantations [50]. Due to their generalist diet, these foxes can easily find food resources in forested and open habitats [50,51]. Despite *M. tridactyla* feeding mainly on terrestrial ants from the genera *Atta*, *Ectatoma*, and *Solenopsis* [42, 43], they are often associated with open vegetation formations [40] and anthropogenic habitats such as plantations [52]. Their use of open areas is linked to thermoregulation, as giant anteaters tend to be active in less-covered habitats on colder days to expose themselves to solar radiation [13, 53].

In the case of *O. virginianus cariacou*, this cervid displays a high tolerance to human disturbance [54], allowing it to use different habitats as long as they provide three key resources: water, cover, and food [55, 56]. Given that its diet can vary based on sex, life stage, season, and reproductive stage [55, 57–59], it can feed on different herbs, forbs, and shrubs highly available in open savannas [60]. Nevertheless, this cervid can also complement its diet by foraging on other plant species in forests where it can rest, find refuge, and access riverbanks [61]. Studies in Mexico have found that white-tailed deer prefer open savannas due to the abundance of cover provided by shrubs and the high plant diversity in their diet [60]. However, other studies have suggested that these cervids prefer well-preserved forests where they can find plants that fulfill their basic requirements [55]. Our work reveals that *O. virginianus cariacou* can use gallery forests and open savannas in Arauca and Casanare (Fig. 2), highlighting the importance of conserving both habitats for this species.

Although analyzing variation in habitat preferences between sites was beyond our study's scope, *T. tetradactyla* and *O. virginianus cariacou* revealed consistent habitat use patterns between sites, whereas, as discussed earlier, *M. tridactyla* showed variable habitat preferences between sites. This variation may be attributed to differences in predation risk, the natural composition of forests and savannas, and specific land-use conditions at each site, suggesting that species preferences and interactions are site-dependent [19]. Furthermore, it is important to note that our sampling was conducted at the end of the wet season, without considering seasonal variations in habitat use and preference. Future studies should examine how seasonality and related factors modulate habitat use and preference of terrestrial mammals in Neotropical floodplain savannas.

5. Conclusions

Our findings emphasize the importance of conserving gallery forests and natural open savannas to sustain medium and large-sized mammals in the Colombian Llanos. Although gallery forests are heavily used and preferred by most mammal species, some complement their resource needs in open natural savannas. Therefore, both habitats should be integrated into regional conservation strategies. Given that protected areas are underrepresented in the Colombian Llanos [62], it is essential to promote alternative conservation strategies encouraging landowners to preserve these habitats, thereby ensuring long-term protection for mammal biodiversity.

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7. Conflict of interest

The authors declare that there are no conflicts of interest.

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Los bosques de galería y las sabanas abiertas son hábitats clave para los mamíferos terrestres en los Llanos Colombianos

Resumen: Las condiciones del hábitat son fundamentales para proporcionar los requisitos esenciales de las especies de mamíferos y garantizar su viabilidad en las comunidades naturales. Los Llanos Colombianos albergan una alta biodiversidad de mamíferos; sin embargo, pocos estudios han abordado aspectos clave de la historia natural de esta región, como el uso y la preferencia de hábitat. Es este estudio, evaluamos el uso de bosques de galería y sabanas abiertas por parte de mamíferos de tamaño mediano y grande en dos localidades de los Llanos Colombianos, analizando las preferencias de hábitat de las distintas especies con la hipótesis de que éstas utilizarían y preferirían los bosques de galería por encima de las sabanas abiertas. Instalamos 60 cámaras trampa en dos sitios durante 35 días (2100 días-cámara trampa), cubriendo hábitats tanto de bosques de galería como de sabanas abiertas. Las abundancias relativas de las especies detectadas fueron sometidas a análisis de Chi-cuadrado e intervalos de confianza de Bonferroni al 95 % para evaluar el uso y preferencia de hábitat. Todas las especies de mamíferos registradas utilizaron los bosques de galería, y el $\approx$ 50 % de ellas usaron exclusivamente este hábitat. La mayoría de los mamíferos mostró preferencia por los bosques, aunque algunas especies encontraron recursos complementarios en las sabanas abiertas. Solo los chigüiros mostraron una preferencia significativa por la sabana abierta. Destacamos la importancia de conservar los bosques de galería y las sabanas abiertas en los Llanos Colombianos para mejorar condiciones de hábitat que garanticen la supervivencia de los mamíferos. Se debe incentivar a los propietarios de tierras a implementar iniciativas de conservación que aseguren la protección a largo plazo de las áreas naturales requeridas por estas especies.

Palabras Clave: cámaras trampa; cuenca del Orinoco; mamíferos neotropicales; preferencia de hábitat; uso del hábitat.

As florestas de galeria e as savanas abertas são habitats-chave para os mamíferos terrestres nos Llanos Colombianos

Resumo: As condições do habitat são essenciais para suprir as necessidades das espécies de mamíferos e garantir sua sobrevivência nas comunidades naturais. Os Llanos Colombianos abrigam uma alta biodiversidade de mamíferos; no entanto, poucos estudos abordaram aspectos-chave da história natural dessa região, como o uso e a preferência de habitat. Neste estudo, avaliamos o uso de florestas de galeria e savanas abertas por mamíferos de médio e grande porte em duas localidades dos Llanos Colombianos, analisando as preferências de habitat das diferentes espécies com a hipótese de que estas utilizariam e prefeririam as florestas de galeria em relação às savanas abertas. Instalamos 60 armadilhas fotográficas em dois locais durante 35 dias (2100 dias-câmera), cobrindo habitats tanto de florestas de galeria quanto de savanas abertas. As abundâncias relativas das espécies detectadas foram submetidas a análises de Qui-quadrado e intervalos de confiança de Bonferroni a 95 % para avaliar o uso e preferência de habitat. Todas as espécies de mamíferos registradas utilizaram as florestas de galeria, sendo que ≈ 50 % delas utilizaram exclusivamente esse habitat. A maioria dos mamíferos demonstrou preferência pelas florestas, embora algumas espécies tenham encontrado recursos complementares nas savanas abertas. Apenas as capivaras mostraram uma preferência significativa pela savana aberta. Destacamos a importância de conservar as florestas de galeria e as savanas abertas nos Llanos Colombianos para melhorar as condições do habitat e garantir a sobrevivência dos mamíferos. Os proprietários de terras devem ser incentivados a implementar iniciativas de conservação que assegurem a proteção a longo prazo das áreas naturais necessárias para essas espécies.

Palavras-chave: armadilhas fotográficas; bacia do Orinoco; mamíferos neotropicais; preferência de habitat; uso do habitat.

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