UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES ZARAGOZA

ECOLOGÍA

USO DE CUERPOS DE AGUA (SARTENEJAS) POR AVES Y MAMÍFEROS DENTRO Y FUERA DE LA RESERVA DE LA BIOSFERA DE CALAKMUL, MÉXICO

TESIS

POR ARTÍCULO CIENTÍFICO

Using small water deposits (sartenejas) to detect effects of land conservation status on the structure, composition and activity of tropical birds and mammals in Calakmul, Mexico

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

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CIUDAD DE MÉXICO, AGOSTO, 2020

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P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **24 de febrero del 2020** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología** del alumno **DELGADO MARTÍNEZ CARLOS MAURICIO** con número de cuenta **413015525** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Using small water deposits (sartenejas) to detect effects of land conservation status on the structure, composition and activity of tropical birds and mammals in Calakmul, Mexico"**, que es producto del proyecto realizado en la maestría que lleva por título: **"Uso de cuerpos de agua (sartenejas) por aves y mamíferos dentro y fuera de la Reserva de la Biosfera de Calakmul, México"**, ambos realizados bajo la dirección del **DR. EDUARDO MENDOZA RAMÍREZ**, quedando integrado de la siguiente manera:

Presidente:	**DRA. TANIA ESCALANTE ESPINOSA**
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Suplente:	**DRA. ELLEN ANDRESEN**

Sin otro particular, me es grato enviarle un cordial saludo.

Atentamente
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 22 de junio del 2020

POSGRADO EN CIENCIAS BIOLÓGICAS
COORDINACIÓN

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COORDINADOR

c. c. p. Expediente del alumno

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ÍNDICE

RESUMEN

El estudio de la ecología de la fauna silvestre en relación con el uso del recurso agua es fundamental debido a que, como pocos elementos, ésta es esencial para su supervivencia y porque es probable que su disponibilidad se reduzca en un futuro cercano. Este estudio se realizó en la región de Calakmul, México, que a pesar de poseer una abundante vegetación y una fauna de vertebrados diversa, presenta una disponibilidad sumamente limitada de agua. Se tiene identificadas a las aguadas como una fuente fundamental de agua para la fauna que habita en esta región, sin embargo, recientemente se ha encontrado que cuerpos de agua más pequeños, conocidos localmente como "sartenejas", pueden también ser una fuente valiosa de este líquido para un amplio conjunto de especies de vertebrados. No obstante, existe aún poca información sobre cómo se compara el uso que la fauna hace de estos cuerpos de agua con el que hace de las aguadas y mucho menos se sabe del impacto que la presencia humana tiene en los patrones de uso de las sartenejas por la fauna. Se instalaron cámaras trampa con el fin de registrar a las especies de aves y mamíferos que visitaron las sartenejas dentro y fuera de la Reserva de la Biosfera de Calakmul (RBC). Se evaluó la respuesta de la riqueza, composición y comportamiento de las especies de aves y mamíferos que usaron el agua contenida en las sartenejas fuera de la RBC. Se detectó una riqueza similar de especies de aves dentro y fuera de la RBC, sin embargo, dentro de la RBC se registró a un mayor número de especies que se conoce son poco tolerantes a la actividad humana, pero no hubo cambio en los patrones de uso de las sartenejas a lo largo del día. En comparación, no se detectaron diferencias en la riqueza de mamíferos nativos, pero sí se observaron diferencias entre la composición de los ensamblajes con una mayor presencia de especies exóticas fuera de la RBC. Además, algunas especies de mamíferos mostraron una disminución en su frecuencia

de uso de las sartenejas fuera de la RBC y en la mayoría de las especies existió un contraste en las horas de uso de las sartenejas fuera y dentro de la RBC. Los resultados de este estudio muestran que existen efectos diferenciados de la presencia humana sobre los patrones de uso de las sartenejas por aves y mamíferos. El monitoreo de sitios como las sartenejas, que proporcionan recursos limitantes, luce como un enfoque efectivo para detectar respuestas a los impactos antrópicos en una variedad amplia de especies. Esto es particularmente importante en una región como Calakmul que destaca por su gran biodiversidad, pero también por la creciente influencia de la presencia humana.

ABSTRACT

A better understanding of how wildlife uses the resource water is greatly needed due to the fact it essential for its survival and because it is expected to suffer significant reduction in its availability in the near future. This study was conducted in the Calakmul region located in the Yucatan Peninsula, Mexico, which supports an exuberant vegetation and a very diverse vertebrate fauna despite sources of water are scarce. Seasonal small ponds, locally known as "aguadas", are known to be an important source of freshwater for wildlife in the Calakmul region but, recent evidence shows that small depressions in the epikarst which fill with rainfall, locally known as "sartenejas", are also an important source of water for a great variety of vertebrate species. There is little information allowing to know how important sartenejas are as a source of freshwater for wildlife in comparison with aguadas, and even less is known about how anthropogenic activities affect use of sartenejas by wildlife. I set up camera traps to record visitation of bird and mammal species to sartenejas within and outside the Calakmul Biosphere Reserve (CBR). I assessed how land conservation status (protected vs. unprotected) affects the diversity, composition and behavior of medium- and large-sized birds and mammals using the *sartenejas* within and outside the CBR. There were only minor differences in species richness in birds recorded using the *sartenejas* within and outside the CBR, but we found differences in species composition in both birds and mammals. More forest specialist bird species were recorded within the CBR. In mammals, these differences included the presence of species such as coyotes and dogs. Only mammals modified their daily activity patterns of use of *sartenejas* outside the CBR as a possible adaptation to reduce contact with humans. The use of small natural features such as sartenejas to monitor vertebrate assemblages is a promising approach to record the presence of species and to

detect impacts of anthropogenic activities on wildlife at the behavioral, population and community level in the Calakmul region.

INTRODUCCIÓN

Durante las últimas décadas, las distintas actividades humanas han generado una alarmante degradación de la naturaleza teniendo entre sus facetas más visibles la drástica disminución de las poblaciones de fauna silvestre y en varios casos incluso su extinción (Dirzo et al., 2014; Venter et al., 2016; IPBES, 2019). Aunque esta situación es generalizada, se sabe que no todas las regiones ni todas las especies se encuentran bajo la misma presión (Pimm et al., 2014; Ripple et al., 2017). En particular, el impacto de las actividades humanas se concentra en los trópicos (Venter et al., 2016; Alroy, 2017). En esta región se ha registrado un amplio número de especies de vertebrados medianos y grandes (ca. > 0.5 kg) que se encuentran en peligro de extinción (Hoffmann et al., 2010; Ripple et al., 2017). Por ejemplo, cerca del 60% de las especies de felinos tropicales con un peso mayor a 15 kg y el total de las especies de los órdenes Pholidota y Proboscidea se encuentran fuertemente amenazados (Ripple et al., 2014, 2016).

Además del impacto directo que tienen las actividades humanas sobre la presencia y abundancia de la fauna silvestre, recientemente se ha documentado un conjunto de efectos indirectos sobre los vertebrados terrestres. Por ejemplo, Gaynor y colaboradores (2018) documentaron cómo las actividades humanas tienen un fuerte efecto en el aumento de la actividad nocturna de mamíferos terrestres. Asimismo, se ha mostrado que tanto las actividades letales como las no letales pueden modificar los patrones de uso de un recurso propiciando una menor frecuencia de uso y visitas más cortas (Crosmary et al., 2012; Suraci et al., 2019).

Las principales amenazas para los vertebrados de talla mediana y grande son el cambio de uso de suelo, la sobreexplotación y la introducción de especies exóticas, que se combinan con algunas características intrínsecas de las historias de vida de estas especies (como las bajas tasas reproductivas y amplios ámbitos hogareños) para generar un efecto sinérgico negativo en sus poblaciones (Alroy, 2017; Ripple et al., 2017; Allan et al., 2019). Sin un adecuado manejo de la fauna y los recursos que requieren, existe el riesgo de perder no sólo a una gran cantidad de especies sino también las funciones ecológicas y servicios ecosistémicos que proporcionan, tales como la dispersión y depredación de semillas y el ciclaje de nutrientes (Ripple et al., 2015, 2016).

Una de las principales estrategias que se han adoptado a nivel mundial para la conservación de la biodiversidad son las áreas naturales protegidas (Gray et al., 2016). Sin embargo, en las regiones tropicales estas áreas se encuentran mayormente inmersas en paisajes antropizados, por lo que no están exentas de la presión ejercida por las actividades humanas (Geldmann et al., 2014). Las áreas naturales protegidas han mostrado ser efectivas en el mantenimiento de la riqueza de especies y sus abundancias, pero existe poca información que permita evaluar su papel en preservar atributos de la fauna como sus patrones de forrajeo y de actividad a lo largo del día (Pocock et al., 2015; Gaynor et al., 2018).

En México, una de las áreas naturales protegidas con mayor extensión es la Reserva de la Biosfera de Calakmul (RBC), la cual se encuentra al sureste del estado de Campeche en la Península de Yucatán; esta reserva forma parte del Corredor Biológico Mesoamericano y de la Selva Maya, el segundo bosque tropical más grande de América (Gómez-Pompa et al., 1995; Nations, 2006). A pesar de poseer una exuberante vegetación tropical, la Península de Yucatán cuenta con pocos cuerpos de agua superficiales perennes que puedan ser utilizados como fuente de abastecimiento tanto por humanos como por la fauna silvestre (Torrescano-Valle y Folan, 2015). Esto se debe a la geología kárstica de la región que hace que la mayor parte del agua se infiltre al subsuelo, generando una red de cuerpos de agua subterráneos (Back y Lesser, 1981; Gelting, 1995). El agua, como recurso limitante, ha sido vinculada a distintos procesos ecológicos como fluctuaciones en los tamaños poblacionales de vertebrados en zonas desérticas y semidesérticas (Gandiwa et al., 2016), así como a los patrones de movimiento de los mamíferos en ecosistemas estacionales (Reyna-Hurtado et al., 2012).

Se ha logrado un gran avance en el estudio de los cuerpos de agua localmente conocidos como "aguadas" (acumulaciones de agua pluvial en depresiones topográficas con suelos impermeables) en la región de Calakmul y se ha reconocido que son altamente relevantes para un gran número de especies (Back y Lesser, 1981; Reyna-Hurtado et al., 2010, 2012, 2019; Sandoval-Serés et al., 2016). Sin embargo, resulta imprescindible entender el rol que otros reservorios de agua juegan para el mantenimiento de la fauna silvestre. Por ejemplo, existen cuerpos de agua de menor tamaño, localmente conocidos como "sartenejas" (formados por la acumulación de lluvia en oquedades naturales que se forman por la erosión del suelo rocoso), que recientemente se ha documentado son utilizados por un amplio conjunto de especies de aves y mamíferos (Flores, 1983; Delgado-Martínez et al., 2018). Es de particular relevancia entender los patrones de uso de los cuerpos de agua por parte de la fauna silvestre por la posibilidad de que ocurran periodos prolongados sin lluvias y aumentos de la temperatura en la región de Calakmul debido al cambio climático (Mardero et al., 2012, 2020). Además, el contar con información precisa sobre este tema puede ayudar a generar estrategias de manejo que permitan mitigar los efectos derivados de la creciente presión de las actividades humanas sobre la biodiversidad de la región (O'Farril et al., 2014; Paredes et al., 2017).

El objetivo principal del presente estudio fue evaluar el impacto del estado de protección de dos sitios (i.e., dentro y fuera de la RBC) sobre la diversidad, composición de especies y comportamiento de aves y mamíferos medianos y grandes que hacen uso de las sartenejas como una fuente de agua en la región de Calakmul. Tomando en cuenta la información previa, formulo las siguientes hipótesis y predicciones sobre el impacto del estado de protección sobre las aves y mamíferos que hacen uso de las sartenejas:

1) La diversidad y composición de los ensamblajes de aves y mamíferos que hacen uso de las sartenejas será diferente dentro y fuera de la RBC, se espera que esto sea resultado de la extirpación o disminución de abundancia de especies poco tolerantes al disturbio antropogénico y la presencia de especies exóticas fuera de la RBC,

2) Las aves y mamíferos que hacen uso de las sartenejas modificarán distintos aspectos de su comportamiento con el fin de evitar las actividades humanas que se realizan fuera de la RBC. Se espera una disminución en la frecuencia de uso, visitas más cortas y cambios en los patrones de uso de las sartenejas a lo largo del día.

El presente documento está conformado por: a) esta introducción, b) un manuscrito enviado a la revista *Biological Conservation* que se enfoca en evaluar cómo contrastan los patrones de uso de las sartenejas por aves y mamíferos dentro y fuera de la RBC y c) una breve discusión final.

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Abstract

The Calakmul Region in the Yucatan Peninsula, Mexico, is a recognized biodiversity hotspot of vertebrate fauna, under increasing pressure from human activities. In this seasonal tropical forest, small water deposits locally known as sartenejas are a focus of animal activity and thus offer a great opportunity to record their presence and behavior. In this study, we used sartenejas as monitoring sites to examine the effects of land conservation status (within vs. outside the Calakmul Biosphere Reserve, CBR) on the characteristics of bird and mammal assemblages (species richness and composition) and species behavior (use intensity and daily activity pattern). We recorded a total of 23 bird and 25 mammal species visiting sartenejas. We did not detect differences in bird species richness within and outside the reserve but there were differences in species composition. In contrast, mammal species richness was slightly lower within the CBR but there were no significant differences in species composition. However, mammals modified their behavior (daily activity pattern) outside the reserve as a possible adaptation to reduce contact with humans. The use of small natural features such as sartenejas to monitor vertebrate assemblages is a promising approach to detect impacts of human activity on wildlife at the behavioral, population and community level in the biodiversity hotspot of the Calakmul Region.

Keywords	Camera-trapping; natural protected areas; tropical forest; wildlife monitoring; water bodies; Selva Maya.

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Using small water deposits (*sartenejas*) to detect effects of land conservation status on the structure, composition and activity of tropical birds and mammals in Calakmul, Mexico

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Highlights

- Small water deposits (*sartenejas*) concentrate wildlife activity in Calakmul, Mexico.
- Land protection status affects differentially birds and mammals visiting *sartenejas*.
- Composition of bird assemblages change, whereas mammals modify their daily activity pattern.
- *Sartenejas* provide an ideal setting to monitor human impacts on wildlife.

Abstract

The clear understanding of the magnitude of the intense pulse of vertebrate defaunation that is affecting tropical forests worldwide requires an integrated approach for assessing its impact from the individual to the community level. The Calakmul region in the Yucatán Peninsula, Mexico, is a biodiversity hotspot of vertebrate fauna, which is under increasing pressure because of anthropogenic activities. Water scarcity in the region makes small water deposits, locally known as *sartenejas*, ideal places for recording vertebrate presence and behavior. We used camera traps to monitor *sartenejas* and examine the effects of land conservation status (within vs. outside the Calakmul Biosphere Reserve) on the characteristics of bird and mammal assemblages (species richness and composition), as well as species behavior (intensity and daily activity patterns of water use). We recorded a total of 19 bird and 24 mammal species using the *sartenejas*. There were only minor differences in species richness in birds recorded using *sartenejas* within and outside the reserve, but we found differences in species composition in both birds and mammals. In mammals, these differences included the presence of species such as coyotes and dogs. Only mammals modified their daily activity patterns of *sartenejas* use outside the reserve. Focusing our survey on *sartenejas* allowed us to record a large proportion of the medium- and large-sized bird and mammal fauna occurring in the region and to document the variation in their response to perturbation among groups (birds vs. mammals) and among species within groups. Because of the current governmental plans to develop a large infrastructure project in the region and the likely reductions in water supply caused by the expected changes in climate patterns, the type of information generated in this study is key in having a baseline for better understanding and assessing the impact on the wildlife in a timely manner.

Key words: camera trapping, protected areas, tropical forest, wildlife monitoring, water bodies, Selva Maya.

1. Introduction

Anthropogenic activities are exerting an unprecedented pressure on natural environments, threatening to drive nearly 1 million species to extinction within the coming decades (Dirzo et al., 2014; Pimm et al., 2014; Venter et al., 2016; IPBES, 2019). Protected areas are one of the main conservation tools for reducing human pressures on natural habitats (Gray et al., 2016). In tropical forests, however, where a large proportion of global biodiversity is concentrated, protected areas are becoming increasingly isolated and immersed in human-dominated landscapes, which poses a serious risk to the long-term conservation of native species that depend on natural habitats to maintain stable populations (Geldmann, Joppa, & Burgess, 2014; Allan et al., 2019).

Mammal and bird species perform important ecological functions in tropical forests, some of these functions are directly linked to forest regeneration (Stoner et al., 2007; Bregman et al., 2016; Gardner et al., 2019). Several of these species, however, are highly sensitive to the effects of anthropogenic activities because of some of their life history traits, such as large home ranges, small litter size and long gestation periods (Ripple et al., 2017). There is evidence indicating that anthropogenic activities have the potential to affect wildlife at different levels, ranging from the diversity and composition of their communities to the abundance of their populations and even the behavior of their individuals (Pimm et al., 2014; Venter et al., 2016; Ripple et al., 2017; Benítez-López, 2018). Most of the research documenting human impact on wildlife, however, has focused on attributes such as species richness and abundance, whereas few studies have attempted to simultaneously evaluate impact at different levels (from behavior to community composition and richness) (Steidl & Powell, 2006; Carmel et al., 2013). The full understanding of the magnitude and consequences of anthropogenic activities on wildlife requires examining their responses at these multiple levels.

Small natural features where wildlife activity concentrates (e.g., fruiting trees, mineral licks and water bodies) provide ideal places for simultaneously recording information on animal diversity, composition, abundance and behavior (Matsubayashi et al., 2007; Vale, Pimm, & Brito, 2015; Camargo-Sanabria & Mendoza, 2016; Hunter, 2017). Nevertheless, few studies have taken advantage of these natural features to assess the impact of anthropogenic activities on bird and mammal communities, populations and individuals (e.g., Blake, Mosquera, & Salvador, 2013; Briceño-Méndez et al., 2016; Eaton et al., 2017).

The role of water bodies as hotspots of wildlife activity is well-known from dry environments (Davis, Kerezsy, & Nicol, 2017), but even in ecosystems supporting lush vegetation, water can exist in a very limited supply for the fauna (Okahisa et al., 2015). This is the case for tropical forests growing in karst soils in the Yucatán Peninsula in Mexico, in which aboveground rivers and extensive water bodies are scarce (García-Gil, Palacio-Prieto, & Ortiz-Pérez, 2002; Torrescano-Valle & Folan, 2015). Nevertheless, this region supports one of the most diverse vertebrate faunas in Mesoamerica (Calmé et al., 2015; Charruau, Cedeño-Vázquez, & Köhler, 2015; Reyna-Hurtado et al., 2015). Among the few terrestrial water bodies present in the region, seasonal waterholes, known locally as *aguadas*, were considered to be the main source of fresh water for wildlife in a large proportion of the peninsula (Back, 1995; Reyna-Hurtado et al., 2010; Fig. S1a). Recent evidence shows, however, that sartenejas, small depressions in the epikarst that fill with rainfall, are also an important source of water for a great variety of vertebrate species, a characteristic that in combination with their relatively small size (usually less than 4 m^2) makes them ideal spots for recording wildlife activity (Delgado-Martínez et al., 2018; Fig. S1b).

In this study, we assess how land conservation status (protected vs. unprotected) affects the diversity, composition and behavior of medium- and large-sized birds (> 170 g) and terrestrial mammals (> 450 g) using *sartenejas* in the Calakmul region in southern Mexico. We expect that bird and mammal assemblages using *sartenejas* within the Calakmul Biosphere Reserve (CBR) will show differences in species richness and composition that reflect the loss of species sensitive to anthropogenic disturbance and the arrival of non-native fauna (e.g., cattle and dogs), when compared with the faunal assemblages using *sartenejas* outside the CBR. Moreover, we expect that birds and mammals using *sartenejas* will have a lower frequency of visitation, shorter visits, and changes in their daily activity patterns outside the CBR. These changes in daily activity patterns are expected to reflect adjustments to avoid hours of greater anthropogenic activity.

2. Materials and Methods

2.1. Study site

Fieldwork was conducted in the southern portion of the CBR and communal lands of the *Nuevo Conhuas* village, both located in the Calakmul region, in the state of Campeche in southern Mexico (Fig. S2). The Calakmul region extends 2,000,000 ha and is part of the Mesoamerican Biological Corridor and the Selva Maya; this last is the second largest tract of tropical forest in the Americas (Gómez-Pompa & Dirzo, 1995; Galindo-Leal, 1999;

Nations, 2006). The climate in this region is tropical and subhumid with summer rains (between June and September) and a dry winter (between December and March). The mean annual precipitation is 1059 mm (CONAGUA, 2010). The CBR was established in 1989 and has a total extent of 723,185 ha (Gómez-Pompa & Dirzo, 1995). The CBR is a stronghold for several endangered species both at the national and the global level such as *Spizaetus ornatus*, *Crax rubra*, *Tapirus bairdii*, *Tayassu pecari* and *Panthera onca* (Calmé et al., 2015; Charruau, Cedeño-Vázquez, & Köhler, 2015; Naranjo et al., 2015; Reyna-Hurtado et al., 2015). Anthropogenic activities within the CBR are restricted to ecotourism and biological and archeological research. The communal lands of the *Nuevo Conhuas* extend approximately 56,400 ha and are located in the vicinity of the CBR (Fig. S2). Productive activities in this community include cattle ranching, beekeeping, subsistence farming and hunting (Calmé & Guerra, 2005; Delgado-Martínez, pers. obs.).

2.2. Selection and monitoring setup of sartenejas

Our focal *sartenejas* were located in the southern portion of the CBR (hereafter "within the reserve") and in the communal lands of the *Nuevo Conhuas* (hereafter "outside the reserve") (Fig. S2). We recorded the location of 20 *sartenejas* within the reserve, including 2 *sartenejas* previously reported by Reyna-Hurtado et al. (2012) and 18 *sartenejas* that were recorded during walks with local guides, conducted along 26 transects with a total length of 116.6 km. Outside the reserve we located 10 *sartenejas* with the help of local guides, these *sartenejas* were immersed in the forest patches below canopy forest. We selected 10 *sartenejas* for monitoring wildlife, both within and outside the reserve, based on the following criteria: 1) to have a volume of ≥ 20 L and 2) to be located ≥1 km from any other monitored *sarteneja*. The average (± SD) volume (log10 of liters) of s*artenejas* was 1.588 ± 0.203 and 2.125 ± 0.676 within and outside the reserve, respectively, showing a larger volume outside than within the reserve (t = 2.407, df = 10.617, p = 0.036). The average (± SD) distance between *sartenejas* was 7.6 ± 4.23 km and 6.81 ± 3.15 km within and outside the reserve, respectively. Our focal *sartenejas* did not include any previously monitored in Delgado-Martínez et al. (2018).

To verify the homogeneity of associated features to the *sartenejas*, every two months we measured canopy cover around each *sarteneja* using a GRS densitometer™. Additionally, we measured rainfall and temperature during the entire study period using four data-logging rain gauges (placed simultaneously at two *sartenejas* within and two outside the reserve). There were no significant differences in canopy cover (W = 22, p = 0.221), mean monthly temperature (t = 0.751, df = 38, p = 0.457), maximum monthly temperature (t = 1.855, df = 38, p = 0.071), minimum monthly temperature (t = -1.443, df = 38, p = 0.157) neither monthly rainfall (t = 0.022, df = 38, p = 0.983) between *sartenejas* located within and outside the reserve during the study period.

We set up one camera trap at each *sarteneja* and programmed it to take a 20-s long video each time it was activated and to have a 5-s delay before reactivation. We monitored *sartenejas* over a period of 10 months, from April 2018 to January 2019, thereby including the dry and wet seasons. Although we initially monitored a total of 20 *sartenejas,* we only included in the analysis shown below the information from 8 and 9 *sartenejas* within and outside the reserve, respectively, caused by camera trap failure.

2.3. Data analysis

We identified species using the water from the s*artenejas*, discarding only records of *Ateles geoffroyi* from any analysis because this species is primarily arboreal, so most of its activity likely occurred beyond the detection area of our camera traps. We calculated a capture frequency (CF) for each species using the following equation: (the number of events recorded/sampling effort) × 1000 camera days (O'Brien, Kinnaird, & Wibisono, 2003). The events corresponded to single records or grouped records (when they registered the same species in the same camera trap in a short time interval). We grouped animals' records following the procedure described in Camargo-Sanabria & Mendoza (2016).

2.3.1. Differences in the structure and composition of animal assemblages using the sartenejas *within and outside the CBR*

We used different functions from the *vegan* R package to compare the structure and composition of wildlife assemblages using the *sartenejas* (Oksanen et al., 2019). To compare species richness of the bird and mammal assemblages using the *sartenejas* within and outside the reserve, we generated sample-based species' rarefaction curves using the *specaccum* function. We estimated the species richness expected to occur within and outside the reserve by calculating the Chao1 estimator using the *specpool* function. We restricted these analyses to native species.

To compare the composition of bird and mammal assemblages using *sartenejas* within and outside the reserve, we conducted a non-metric multidimensional scaling (NMDS) using the Bray-Curtis index as a measure of distance (calculated based on species CF's) and applying the *metaMDS* function. We performed an analysis of similarities

(ANOSIM) to test for the existence of statistical differences in species composition between assemblages using the *anosim* function. For this analysis we included both native and non-native species.

2.3.2. Differences in the patterns of the use of sartenejas *by birds and mammals within and outside the CBR*

To compare the frequency of use and length of use of *sartenejas* by birds and mammals within and outside the reserve, we performed permutation tests of mean differences using the *infer* R package (Bray et al., 2019). First, we calculated the observed difference in the means of the frequencies and lengths of visitation within and outside the reserve by the focal vertebrate species. Second, we generated a null distribution of mean differences based on 10,000 permutations. In those cases where the observed difference was negative, we calculated the proportion of samples in which the permuted differences were equal to or greater than expected based on the observed difference (*p*-value), but when the observed difference was positive we calculated the proportion of samples in which the permuted differences were equal to or less than expected based on the observed difference (*p*-value). Third, we computed the 95% confidence intervals using 10,000 bootstrap resampling. We restricted this analysis to those species recorded in at least two *sartenejas* in each condition. We compared daily activity patterns of the use of *sartenejas* in those species having at least 10 events within and outside the reserve by applying the Ridout & Linkie (2009) method. Following Meredith & Ridout (2018), we calculated activity overlap using Δ_1 for small samples (less than 75 observations) and Δ_4 for large samples (more than 75 observations).

We used the *basic0* method for the calculation of 95% confidence intervals. All the analyses were conducted using the *overlap* R package (Ridout & Linkie, 2009).

3. Results

We accumulated 3627 camera trap days of sampling, 1712 within the reserve and 1915 outside the reserve. The cameras generated a total of 26,332 videos with at least one animal visible. We were unable to identify the species in less than 1% of these records. We identified a total of 43 species (19 bird and 24 mammal species) using the *sartenejas*: 16 birds and 19 mammals within the reserve and 14 birds and 22 mammals outside the reserve. We recorded another four bird species, however, which had just visited the *sartenejas* but apparently had not used them (Table S1). The species recorded using the *sartenejas* accounted for 44% and 96% of the medium- and large-sized terrestrial birds and mammals, respectively, listed for the Calakmul region. Overall, the most common species recorded using the *sartenejas* were the bird *C. rubra* and the mammal *Dasyprocta punctata*.

3.1. Differences in the structure and composition of animal assemblages using the sartenejas *within and outside the CBR*

The rarefaction curves of bird species were close, but confidence intervals (CI) did not overlap (Fig. S3a). The observed bird richness within the reserve was only slightly lower than expected based on the Chao1 estimator (16 vs. 16.25 ± 0.73, mean ± SE). Outside the reserve, the difference between the observed and estimated richness was slightly larger (14 vs. 16 ± 3.74). The bird species *Chondrohierax uncinatus, Falco columbarius, Penelope purpurascens* and *S. ornatus* were recorded exclusively within the reserve, while *Accipiter* *bicolor*, *Aramides albiventris* and *Buteo plagiatus* were recorded only outside the reserve. Overall, bird assemblages using the *sartenejas* within and outside the reserve were statistically different (ANOSIM $R = 0.908$, $p = 0.001$, Fig. 1a).

The CI of rarefaction curves of mammal species overlapped indicating that richness was similar within and outside the reserve (Fig. S3b). The observed mammal richness within the reserve was lower than the estimated by Chao1 (19 vs. 23.50 ± 7.19), and the observed richness outside the reserve was the same as that estimated by Chao1. Differences between mammal assemblages using the *sartenejas* within and outside the reserve were lower than in the case of birds but still statistically significant (ANOSIM $R = 0.193$, $p = 0.025$, Fig. 1b). Species such as *Mazama temama* and *T. pecari* were recorded only within the reserve, whereas *Canis latrans*, *C. lupus familiaris*, *Herpailurus yagouaroundi*, *Philander opossum* and *Procyon lotor* were recorded only outside the reserve.

3.2. Differences in the patterns of the use of sartenejas *by birds and mammals within and outside the CBR*

The three bird species most frequently recorded using the *sartenejas* within the reserve were, in descending order, *C. rubra*, *Rupornis magnirostris* and *Psilorhinus morio*, whereas outside the corresponding species were the following: *P. morio*, *R. magnirostris* and *Ortalis vetula* (Fig. S4a). The frequency of *sartenejas* use by *C. rubra* decreased by 90% outside the reserve and the length of its visits by 50% (Fig. S5a). In contrast, the frequency of the use of *sartenejas* by *O. vetula*, *P. morio* and *R. magnirostris* increased outside the reserve by nine, six and two times, respectively. The remaining bird species (56% of the total number of evaluated species) showed no difference in their frequency of *sartenejas* use or the length of their visits within versus outside the reserve (Fig. 2a). Bird species using the *sartenejas* had very similar daily activity patterns within and outside the reserve (mean overlap ± standard deviation = 0.785 ± 0.116; Fig. S6).

In the case of mammals, the three most common users of *sartenejas* within the reserve were the following: *Pecari tajacu*, *Leopardus pardalis* and *Urocyon cinereoargenteus*. On the other hand, outside the reserve they were *D. punctata*, *Nasua narica* and *U. cinereoargenteus* (Fig. S4b). *Leopardus pardalis* and *Odocoileus virginianus* reduced their frequency of the use of *sartenejas* to a sixth and a third outside the reserve. In contrast, *Cuniculus paca* and *N. narica* increased their frequency of use four and three times, respectively, outside the reserve. The rest of the evaluated mammal species (69%) showed no changes in their frequency of *sartenejas* use within and outside the reserve (Fig. 2b). The species *C. paca*, *D. punctata* and *N. narica* increased the length of their visits to *sartenejas* outside the reserve by 12, 4 and 2 times, respectively (Fig. S5b).

Differences in daily activity patterns within and outside the reserve were common among mammals, with coefficients of overlap ranging between 0.06 and 0.66 (Fig. 3 and S7). Only *P. tajacu* and *N. narica* were the exceptions. There were different ways in which mammal daily activity was modified. Species such as *L. pardalis*, *O. virginianus* and *Eira barbara* maintained a similar period of activity within and outside the reserve, but the location of their peaks was shifted (Fig. 3a, 3d and S7c). In contrast, *P. concolor* and *M. pandora* changed from being diurnal within the reserve to being mainly nocturnal outside the reserve (Fig. 3b-c). *Cuniculus paca* and *D. punctata* used the *sartenejas* during the same periods within and outside the reserve, but their use was more evenly distributed outside than within the reserve and lacked marked peaks (Fig. S7a-b). Finally, the activity peaks of *U. cinereoargenteus* shifted to earlier hours of the day outside the reserve (Fig. S7f).

4. Discussion

Focusing our survey on *sartenejas* was demonstrated to be an efficient way of recording a large proportion of the medium- and large-sized bird and mammal fauna occurring in the Calakmul region. This wide variety of species provided a sound basis for exploring their response to the impact of anthropogenic activities associated with land conservation status. We were able to detect differences in the response to perturbation of these species both between groups (birds vs. mammals) but also among species within groups.

Interestingly, we did not detect an impact at the level of species richness. This might be partially explained by the occurrence of low deforestation rates in the region (0.12% year^{-1} between 1990 and 2006) and low levels of forest fragmentation (patch density = 0.19/100 ha, total edge length = 47,500 km in 2006) (Ramírez-Delgado, Christman, & Schmook, 2014). Thus, large swaths of natural vegetation remain in the region, which likely helps to buffer the negative impact of human presence on wildlife. Moreover, among the productive activities conducted in the region, those based on cultural practices that do not cause a major change in canopy cover, such as beekeeping, are still common (Calmé & Guerra, 2005; Delgado-Martínez, pers. obs.).

As we shifted the focus of our attention from species richness to assemblage composition and individual behavior, however, we started to find signs of anthropogenic impact. For example, bird species such as *P. purpurascens* and *S. ornatus,* as well as the mammals *M. temama* and *T. pecari,* were only recorded within the reserve, and species such as *C. rubra* and *O. virginianus* were present outside the reserve but suffered an noticeably decrease in their use of *sartenejas*. All these species (with the exception of *S. ornatus*) are heavily hunted locally (Escamilla et al., 2000; Calmé & Guerra, 2005; Reyna-Hurtado & Tanner, 2007; Ripple et al., 2015).

In contrast, three bird and three mammal species (16% and 13% of the total of recorded bird and mammal species, respectively) were recorded only outside the reserve, and another three bird species increased their frequencies of the use of *sartenejas*. Most of the species recorded only outside the reserve and with a neutral or positive response in their frequency of use and length of visits to *sartenejas* share some characteristics. For instance, they are mainly omnivorous, have relatively large litter sizes and are not hunted or chased off by local people (Carrara et al., 2015; Morante-Filho et al., 2015). These traits could therefore aid these species to thrive in human-dominated landscapes (Sol et al., 2014; Samia et al., 2015; Santini et al., 2019).

Additionally, the non-native species *C. latrans* and *C. lupus familiaris* were recorded only outside the reserve. Although the presence of *C. latrans* in southern Mexico has increased over the last few years, people from the *Nuevo Conhuas* village had not recorded it in their communal lands before this study. Thus, its presence has been potentially favored by the farming and cattle ranching activities in the Calakmul region and the animal's ability to take advantage of water provided by *aguadas* and *sartenejas* (Sosa-Escalante et al., 1997; Hody & Kays, 2018). The long tradition of families owning dogs for companionship, hunting and protection during their daily work in the countryside may increase the occurrence of negative interactions with local wildlife through competitive and prey-predator interactions (Hughes & Macdonald, 2013), as some of these dogs can become feral and depend on natural sources of water and food for their survival.

Interestingly, most of the recorded bird species did not modify their daily activity patterns outside the reserve, whereas most of the mammal species showed different daily activity patterns outside as when compared to within the reserve. Disturbance associated with anthropogenic activities outside the reserve, which is more intense during daylight hours, could have generated a new landscape of fear, which might be reinforced by the arrival of exotic predators such as dogs and coyotes (Calmé & Guerra, 2005; Darimont et al., 2015; Clinchy et al., 2016; Suraci et al., 2019). The lack of a similar response in birds might be related to their ability to fly and likely evade low-intensity and short-lasting disturbance events but then revisit the *sarteneja* immediately after (Pomeroy, 1990). Moreover, because the recorded bird species are not hunted (except for *C. rubra*), it is possible that they do not perceive humans as potential predators and are accustomed to their presence (Frid & Dill, 2002; Price, 2008; Sreekar, Goodale, & Harrison, 2015). In fact, it is possible that they are overlapping their daily activity patterns with the period of anthropogenic activities as a way to gain better protection against their natural predators (Berger, 2007; Steyaert et al., 2016).

Alterations in how wildlife uses water (e.g., lower frequencies of use, shorter visits and shifts in daily activity patterns) might have very important consequences for the long-term viability of wildlife populations (Tuomainen & Candolin, 2011; Gaynor et al., 2018). For instance, physiological stress caused by a reduction of water intake might affect animal reproductive success (Wakefield & Attum, 2006; Tuomainen & Candolin, 2011; Zanette et al., 2011; Crosmary et al., 2012). Similarly, changes in the schedule of activity can generate a broad spectrum of negative consequences. For example, temporal shifts in activity might generate maladaptive responses, such as poor navigational capacity and reduced hunting efficiency, which in turn can promote higher metabolic costs and a reduction of individual fitness (Tuomainen & Candolin, 2011; Gaynor et al., 2018; Smith et al., 2018; Suraci et al., 2019).

5. Conclusions and recommendations

Our study shows that even at relatively low to moderate levels human disturbance can have an evident impact on the structure, composition and behavior of wildlife species, which in turn reflects on their water use patterns. In this sense, our findings support the criticisms regarding the high reliance on species richness as the sole indicator of the magnitude of the biological impact of anthropogenic activities (Fleishman, Noss, & Noon, 2006; Dornelas et al., 2014; Newbold et al., 2018). Moreover, our findings are particularly relevant because one of the flagship initiatives of the current Mexican government is to build a train in the Yucatán Peninsula (i.e., the “Mayan train”). It is expected that the Mayan train will attract about 3 million visitors to the region per year, which will likely propel a wave of infrastructure development and the establishment of new human settlements, increasing the demand for resources such as land and water. The increased demand for resources, combined with a very likely decrease in freshwater availability caused by the expected regional increases in temperature and decreases in precipitation as a consequence of global climate change, threaten with causing an accelerated loss of wildlife (Mardero et al., 2012, 2020; Esperon-Rodriguez et al., 2019; IPBES, 2019). A monitoring program focused on *sartenejas* and *aguadas* can be key in providing a baseline for the assessment and early warning of the impact associated with human perturbation.

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Figure captions

Fig. 1 Ordination of *sartenejas* within and outside the Calakmul Biosphere Reserve based on capture frequencies of a) bird and b) mammal species. Ellipses represent 0.95% confidence intervals. Bird species codes: *Acbi = A. bicolor, Aral = A. albiventris, Bupl = B. plagiatus, Buur = B. urubitinga, Chun = C. uncinatus, Civi = C. virgata, Crru = C. rubra, Crci = C. cinnamomeus, Faco = F. columbarius, Leca = L. cayanensis, Meoc = M. ocellata, Miru = M. ruficollis, Mise = M. semitorquatus, Orve = O. vetula, Pepu = P. purpurascens, Psmo = P. morio, Rasu = R. sulfuratus, Ruma = R. magnirostris, Spor = S. ornatus*. Mammal species codes: *Cala = C. latrans, Cafa = C. lupus familiaris, Cose = C. semistriatus, Cupa = C. paca, Dapu = D. punctata, Dano = D. novemcinctus, Dima = D. marsupialis, Divi = D. virginiana, Eiba = E. barbara, Heya = H. yagouaroundi, Lepa = L. pardalis, Mapa = M. pandora, Mate = M. temama, Nana = N. narica, Odvi = O. virginianus, Paon = P. onca, Peta = P. tajacu, Phop = P. opossum, Prlo = P. lotor, Puco = P. concolor, Span = S. angustifrons, Taba = T. bairdii, Tape = T. pecari, Urci = U. cinereoargenteus*.

Fig. 2 Permutation analysis of frequency of use of *sartenejas* by (a) birds and (b) mammals within and outside the Calakmul Biosphere Reserve. Dots and lines represent the observed mean difference and 0.95% bootstrap confidence intervals, respectively. Values located to the left side of the dotted line represent a higher frequency of use of *sartenejas* outside the reserve and vice versa. Statistical differences (p-value < 0.05) are indicated with an asterisk.

Fig. 3 Comparison of daily activity patterns of mammals using *sartenejas* within and outside the Calakmul Biosphere Reserve: a) *L. pardalis*, b) *P. concolor*, c) *M. pandora* and

d) *O. virginianus*. Overlap coefficients with their 0.95% confidence intervals are shown in each case. Gray-shaded areas indicate overlap in activity.

Figures

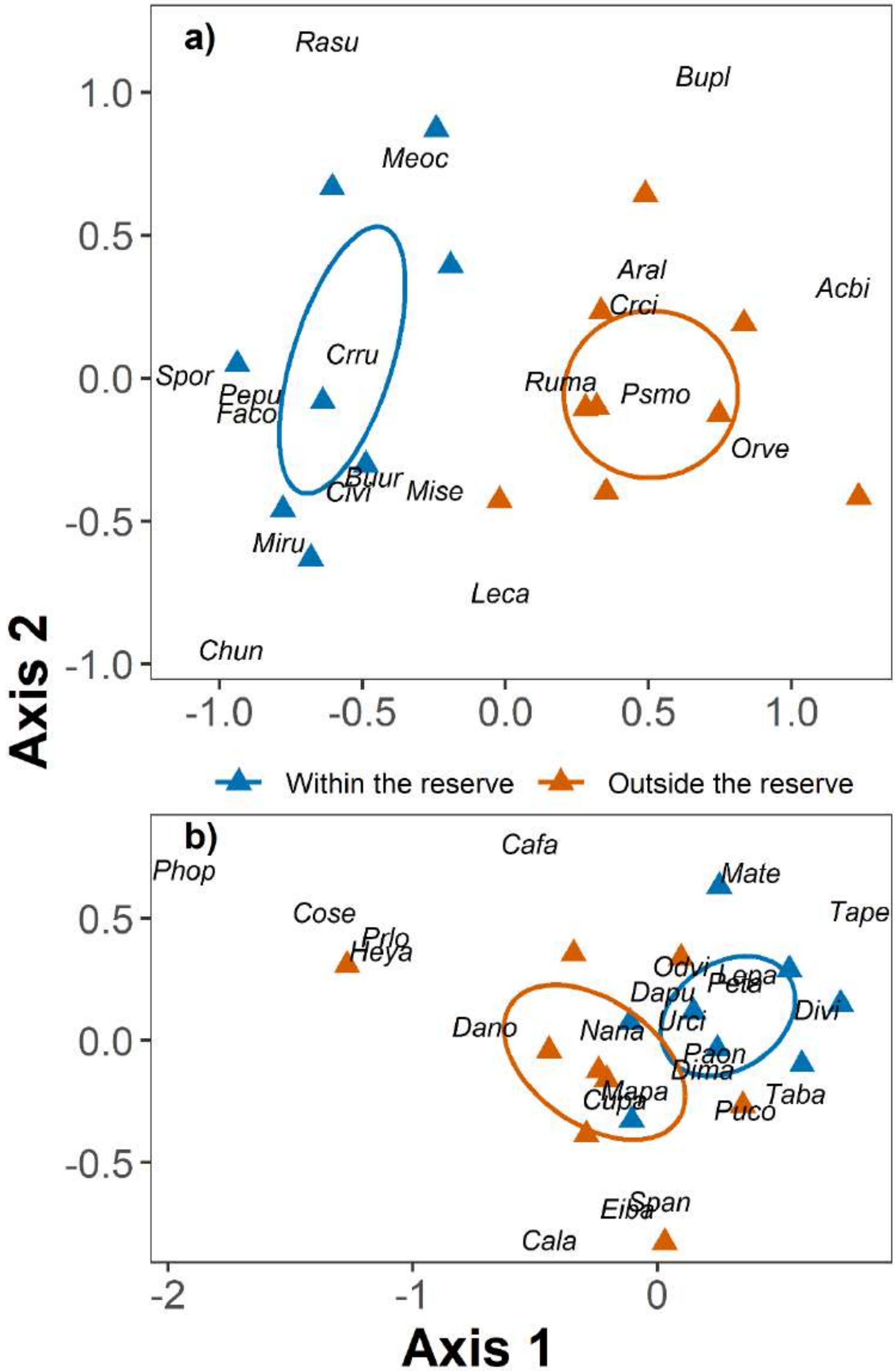


Fig. 1

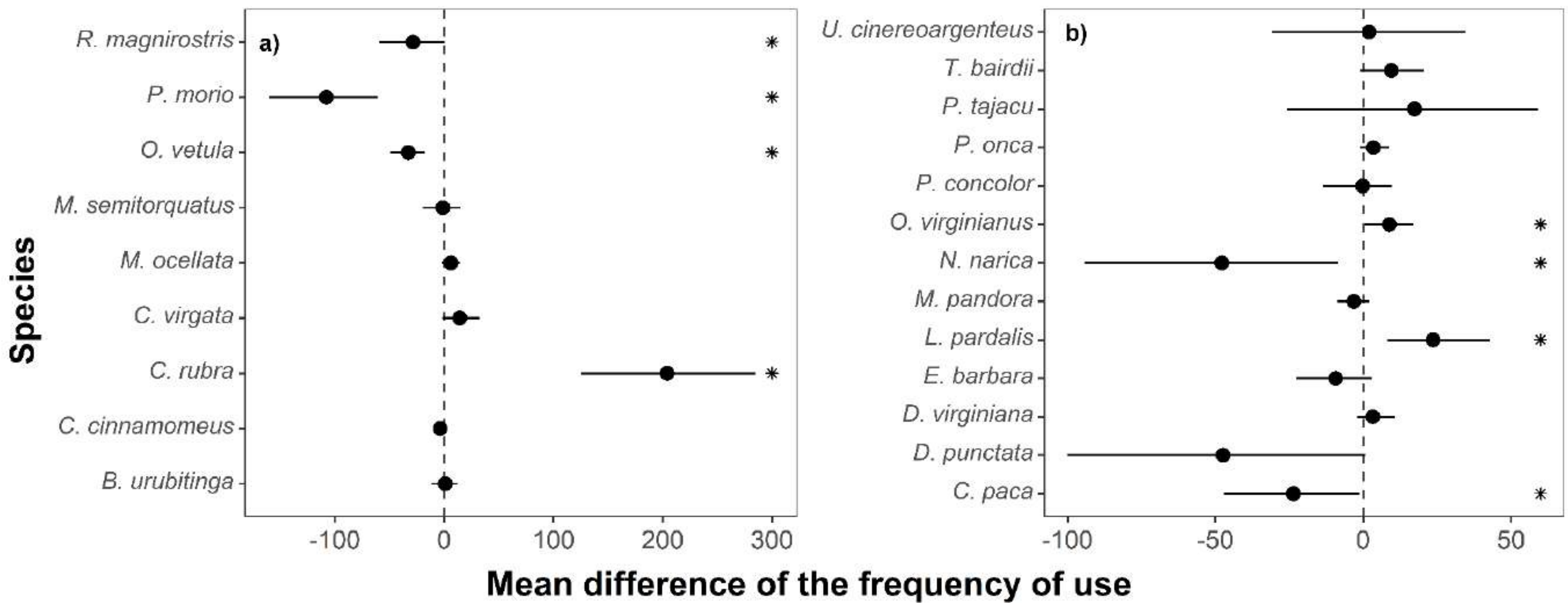

a)
R. magnirostris
P. morio
O. vetula
M. semitorquatus
M. ocellata
C. virgata
C. rubra
C. cinnamomeus
B. urubitinga
-100
0
100
200
300
b)
U. cinereoargenteus
T. bairdii
P. tajacu
P. onca
P. concolor
O. virginianus
N. narica
M. pandora
L. pardalis
E. barbara
D. virginiana
D. punctata
C. paca
-100
-50
0
50
Species
Mean difference of the frequency of use

Fig. 2

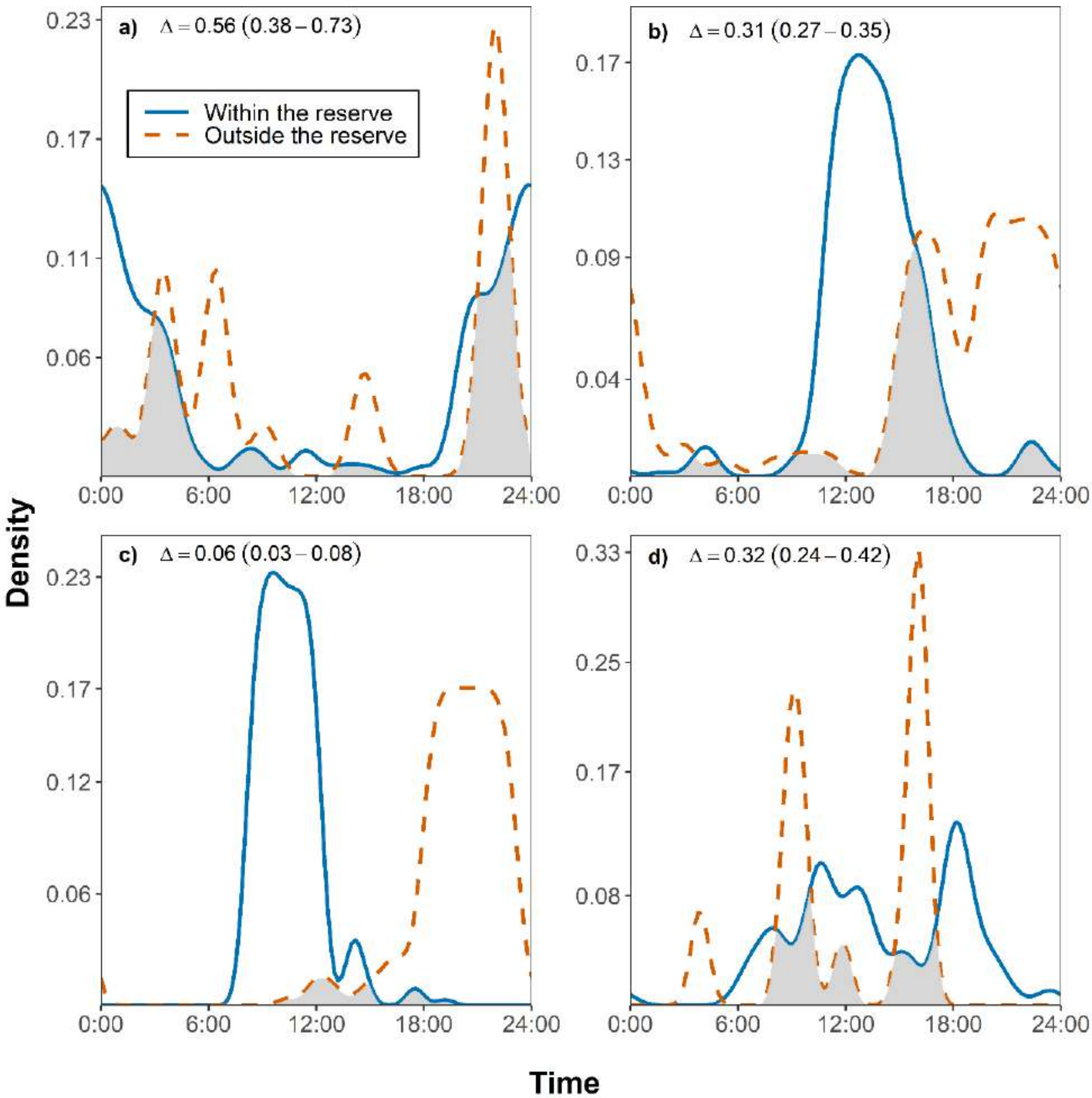

a) Δ = 0.56 (0.38 – 0.73)
Within the reserve
Outside the reserve
b) Δ = 0.31 (0.27 – 0.35)
c) Δ = 0.06 (0.03 – 0.08)
d) Δ = 0.32 (0.24 – 0.42)
Density
Time
0:00
6:00
12:00
18:00
24:00

Fig. 3

Appendix S1

Table S1. Species recorded visiting the *sartenejas* within and outside the Calakmul Biosphere Reserve in Campeche, southern Mexico.

Species	Land conservation status[1]		Level of threat[2]
	Within the reserve	Outside the reserve	
AVES			
Accipiter bicolor	-	B	LC (A)
Aramides albiventris	-	D	LC
Buteo plagiatus	-	D/B	LC
Buteogallus urubitinga	D/B	D/B	LC (Pr)
Chondrohierax uncinatus	B	-	LC (Pr)
Ciccaba virgata	D/B	D/B	LC
Crax rubra	D	D	VU (A)
Crypturellus cinnamomeus	D	D/B	LC (Pr)
Dactylortyx thoracicus	-	None	LC (Pr)
Dryocopus lineatus	None	-	LC
Falco columbarius	B	-	LC
Ictinia plumbea	-	None	LC (Pr)
Leptodon cayanensis	B	B	LC (Pr)
Meleagris ocellata	D	D	NT (A)
Micrastur ruficollis	D/B	D/B	LC (Pr)
Micrastur semitorquatus	D/B	D/B	LC (Pr)

Table S1. Continued.

Species	Land conservation status[1]		Level of threat[2]
	Within the reserve	Outside the reserve	
Ortalis vetula	D	D	LC
Penelope purpurascens	D	-	LC (A)
Psilorhinus morio	D/B	D/B	LC
Pteroglossus torquatus	None	-	LC (Pr)
Ramphastos sulfuratus	D	None	LC (A)
Rupornis magnirostris	D/B	D/B	LC
Spizaetus ornatus	D/B	-	NT (P)
MAMMALIA			
Canis latrans	-	D	LC
Canis lupus familiaris	-	D	-
Conepatus semistriatus	D	D	LC
Cuniculus paca	D	D	LC
Dasyprocta punctata	D/B	D/B	LC
Dasypus novemcinctus	D/B	D/B	LC
Didelphis marsupialis	D	D	LC
Didelphis virginiana	D	D	LC
Eira barbara	D/B	D/B	LC (P)
Herpailurus yagouaroundi	-	D	LC (A)
Leopardus pardalis	D	D	LC (P)

Table S1. Continued.

Species	Land conservation status[1]		Level of threat[2]
	Within the reserve	Outside the reserve	
Mazama pandora	D	D	VU
Mazama temama	D	-	DD
Nasua narica	D/B	D/B	LC
Odocoileus virginianus	D	D	LC
Panthera onca	D	D	NT (P)
Pecari tajacu	D/B	D/B	LC
Philander opossum	-	D	LC
Procyon lotor	-	D/B	LC
Puma concolor	D	D	LC
Spilogale angustifrons	D	D	LC
Tapirus bairdii	D	D	EN (P)
Tayassu pecari	D	-	VU (P)
Urocyon cinereoargenteus	D	D	LC

[1] "B": the animal was inside the *sarteneja* taking a bath, "D": the animal drank *sartenejas* water, "None": the animal was recorded visiting the *sartenejas* but it did not use them, "-": the animal was not recorded visiting the *sartenejas*.

[2] IUCN red list category, "DD": data deficient, "LC": least concern, "NT": near threatened, "VU": vulnerable, "EN": endangered. Between parenthesis it is shown the level of threat at the national level, "A": threatened, "P": endangered, "Pr": under special protection, "-": without category.

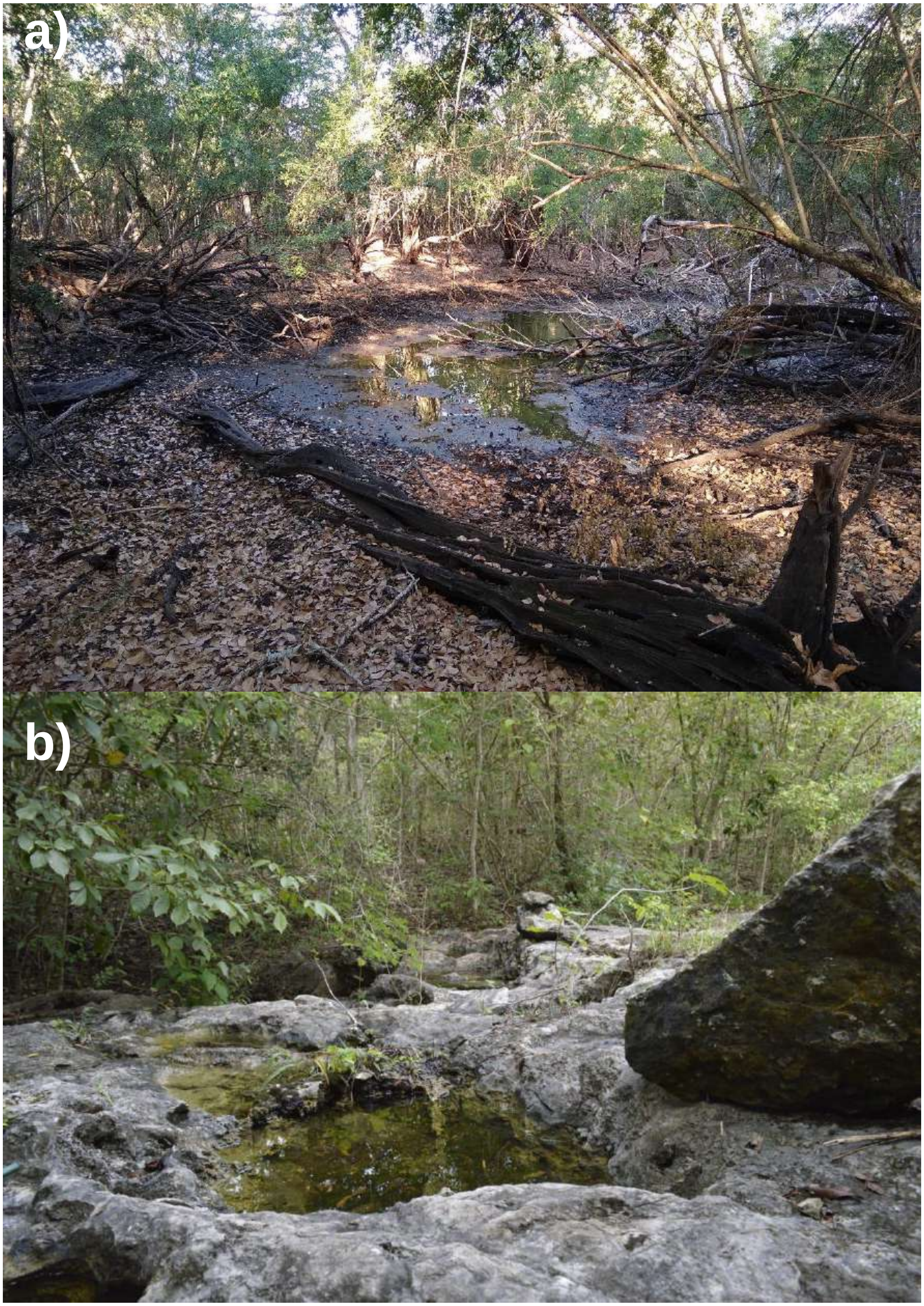


Figure S1. *Aguadas* are accumulations of rainfall at natural depressions on limestone soils (a), photo by C. M. D.-M. *Sartenejas* are small crevices on rocky soils which temporally fill with rainfall (b), photo by T. A.

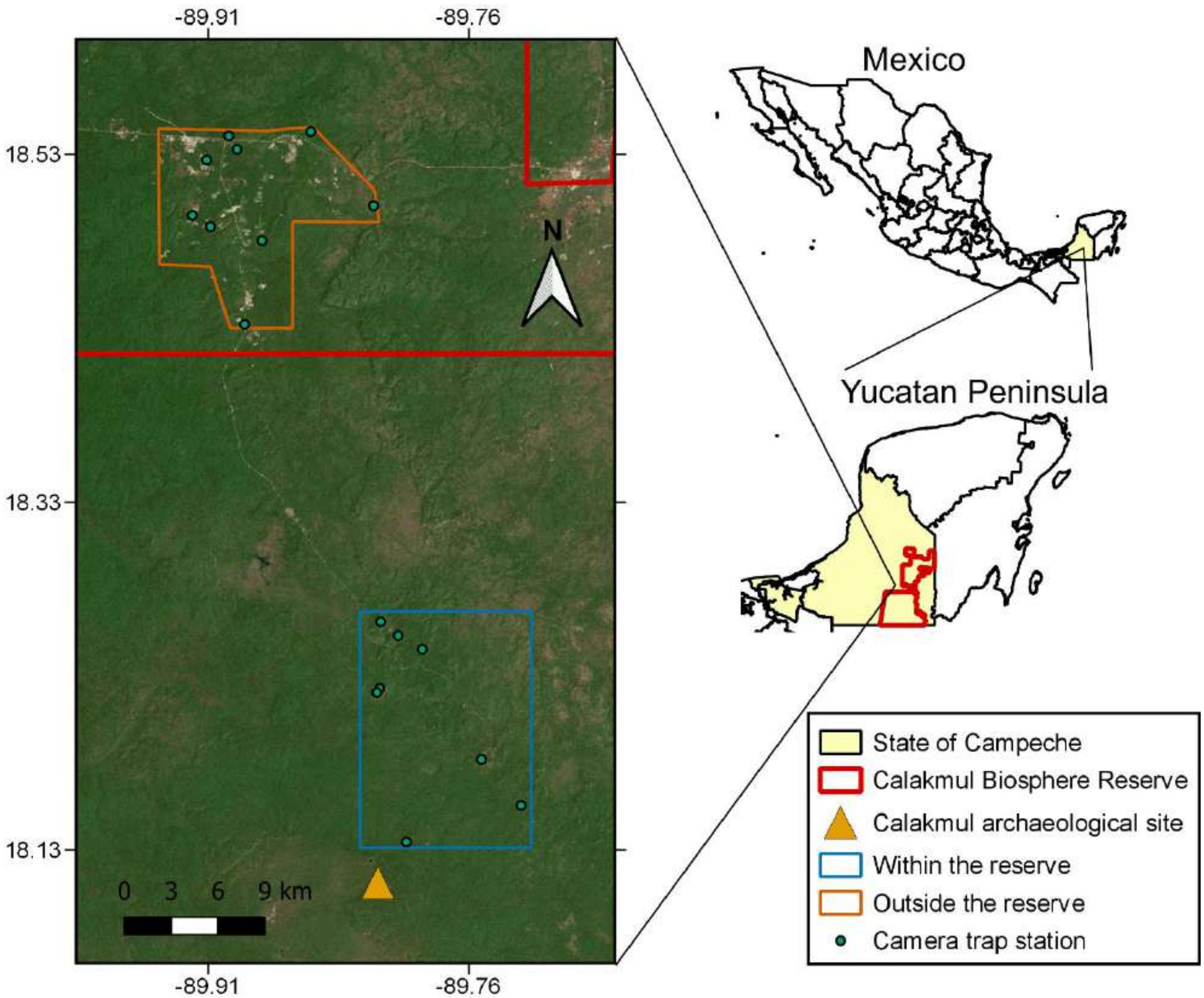


Figure S2. Location of the study area. The orange polygon outside the Calakmul Biosphere Reserve corresponds to the communal lands of "Nuevo Conhuas" village.

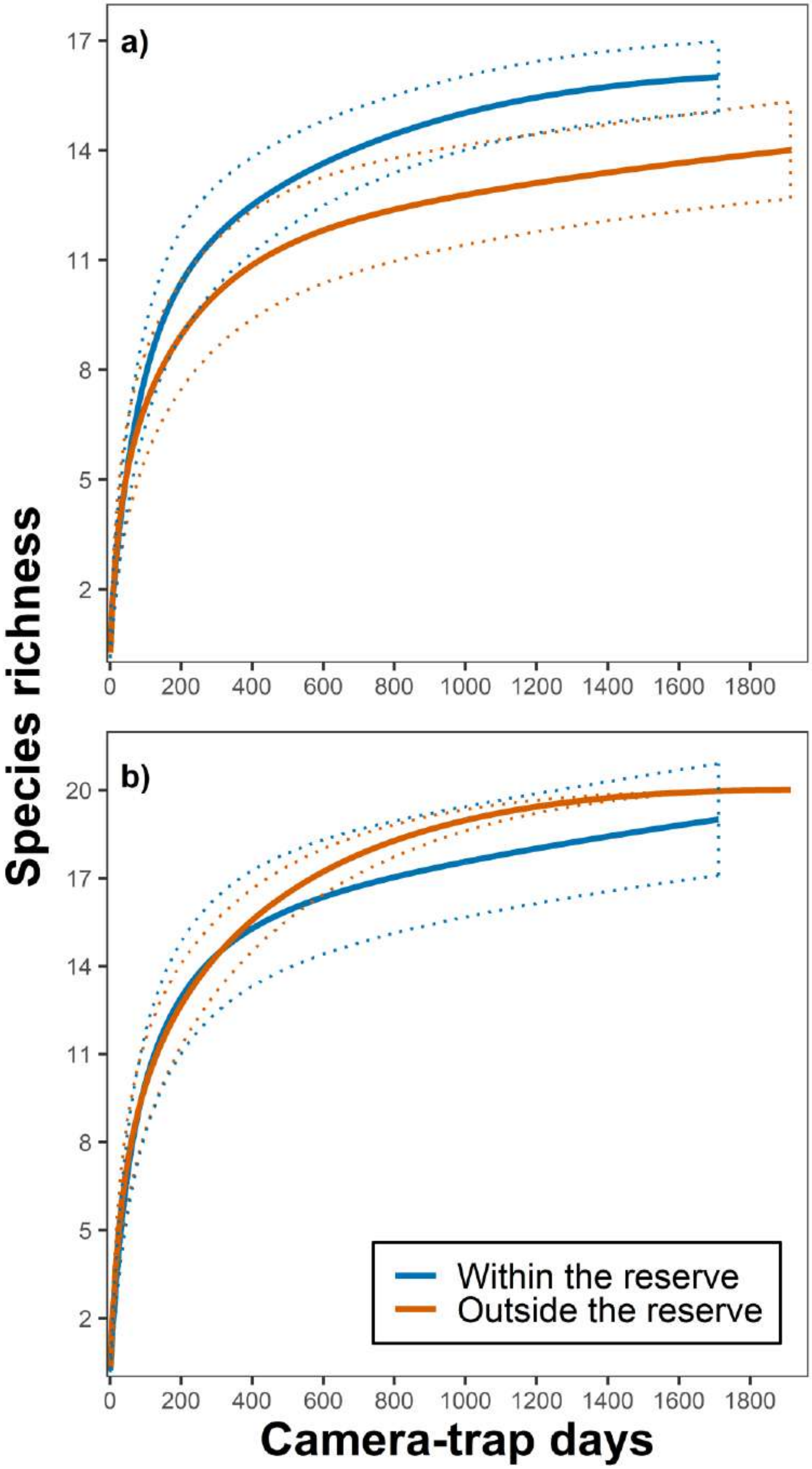


Figure S3. Rarefaction curves of a) bird and b) mammal species using the *sartenejas* within and outside the Calakmul Biosphere Reserve. Dotted lines represent 95% confidence intervals.

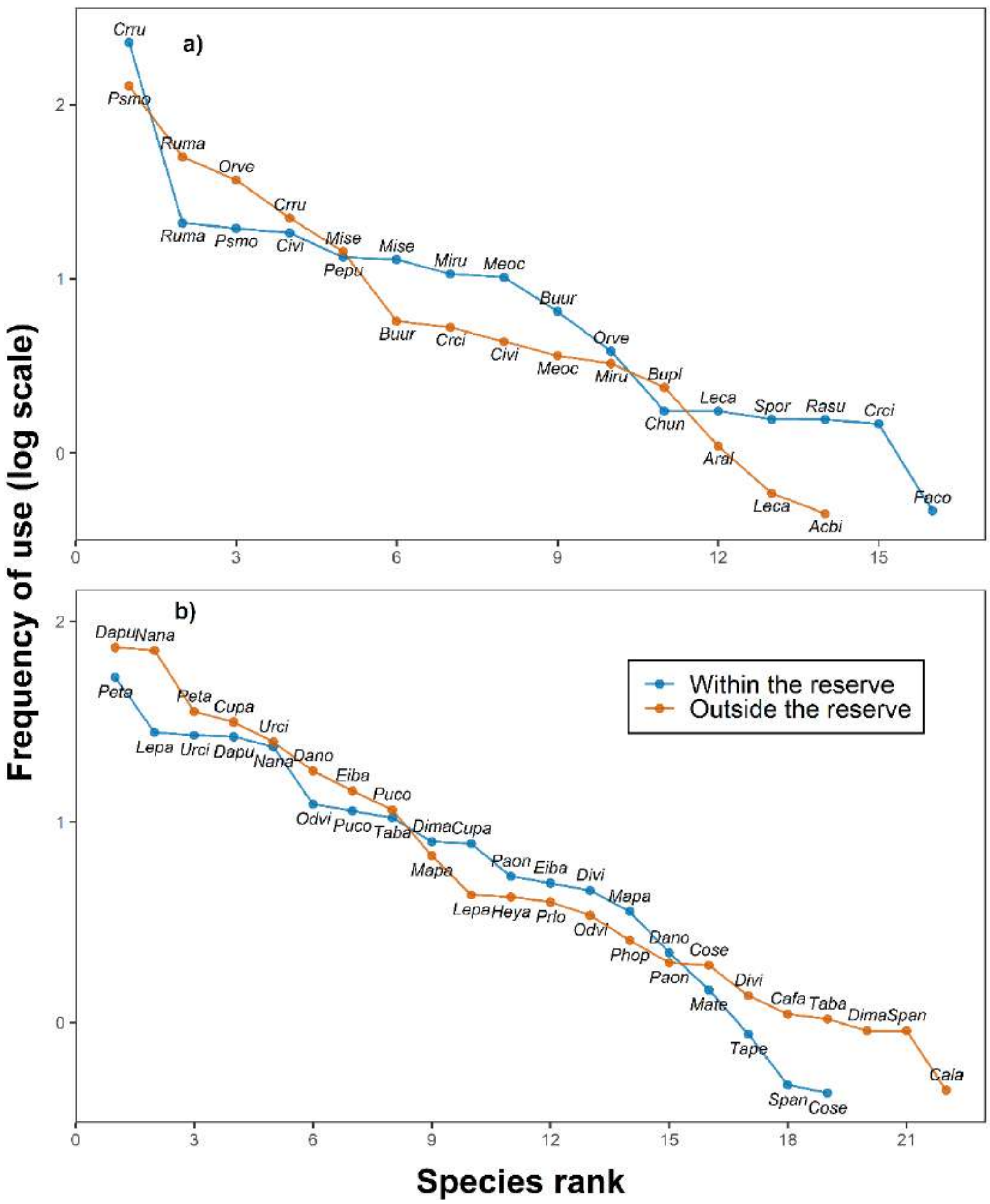


Figure S4. Rank-frequency curves of *sartenejas* use of a) bird species and b) mammal species within and outside the Calakmul Biosphere Reserve. Bird species codes: *Acbi* = *A. bicolor*, *Aral* = *A. albiventris*, *Bupl* = *B. plagiatus*, *Buur* = *B. urubitinga*, *Chun* = *C. uncinatus*, *Civi* = *C. virgata*, *Crru* = *C. rubra*, *Crci* = *C. cinnamomeus*, *Faco* = *F. columbarius*, *Leca* = *L. cayanensis*, *Meoc* = *M. ocellata*, *Miru* = *M. ruficollis*, *Mise* = *M. semitorquatus*, *Orve* = *O. vetula*, *Pepu* = *P. purpurascens*, *Psmo* = *P. morio*, *Rasu* = *R. sulfuratus*, *Ruma* = *R. magnirostris*, *Spor* = *S. ornatus*. Mammal species codes: *Cala* = *C. latrans*, *Cafa* = *C. lupus familiaris*, *Cose* = *C. semistriatus*, *Cupa* = *C. paca*, *Dapu* = *D. punctata*, *Dano* = *D. novemcinctus*, *Dima* = *D. marsupialis*, *Divi* = *D. virginiana*, *Eiba* = *E. barbara*, *Heya* = *H. yagouaroundi*, *Lepa* = *L. pardalis*, *Mapa* = *M. pandora*, *Mate* = *M. temama*, *Nana* = *N. narica*, *Odvi* = *O. virginianus*, *Paon* = *P. onca*, *Peta* = *P. tajacu*, *Phop* = *P. opossum*, *Prlo* = *P. lotor*, *Puco* = *P. concolor*, *Span* = *S. angustifrons*, *Taba* = *T. bairdii*, *Tape* = *T. pecari*, *Urci* = *U. cinereoargenteus*.

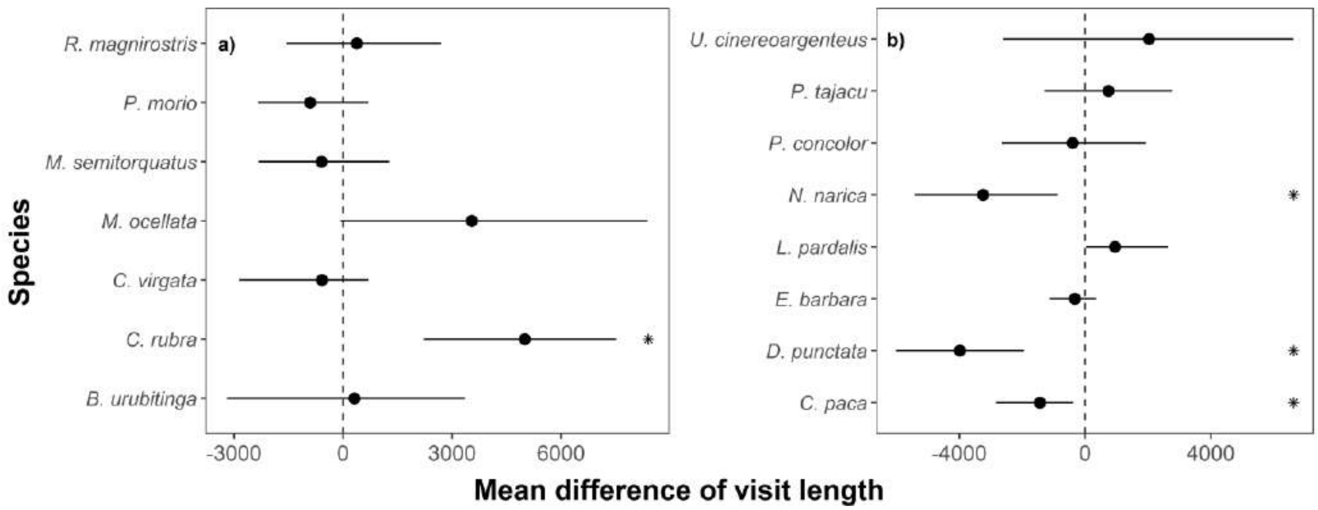


Figure S5. Differences in means of length of use of *sartenejas* of a) birds and b) mammals within and outside the Calakmul Biosphere Reserve. Dots and lines represent the observed mean difference and 0.95% bootstrap confidence intervals, respectively. Values located to the left side of the dotted line represent longer visits outside the reserve and vice versa. Statistical differences (p-value < 0.05) are indicated with an asterisk.

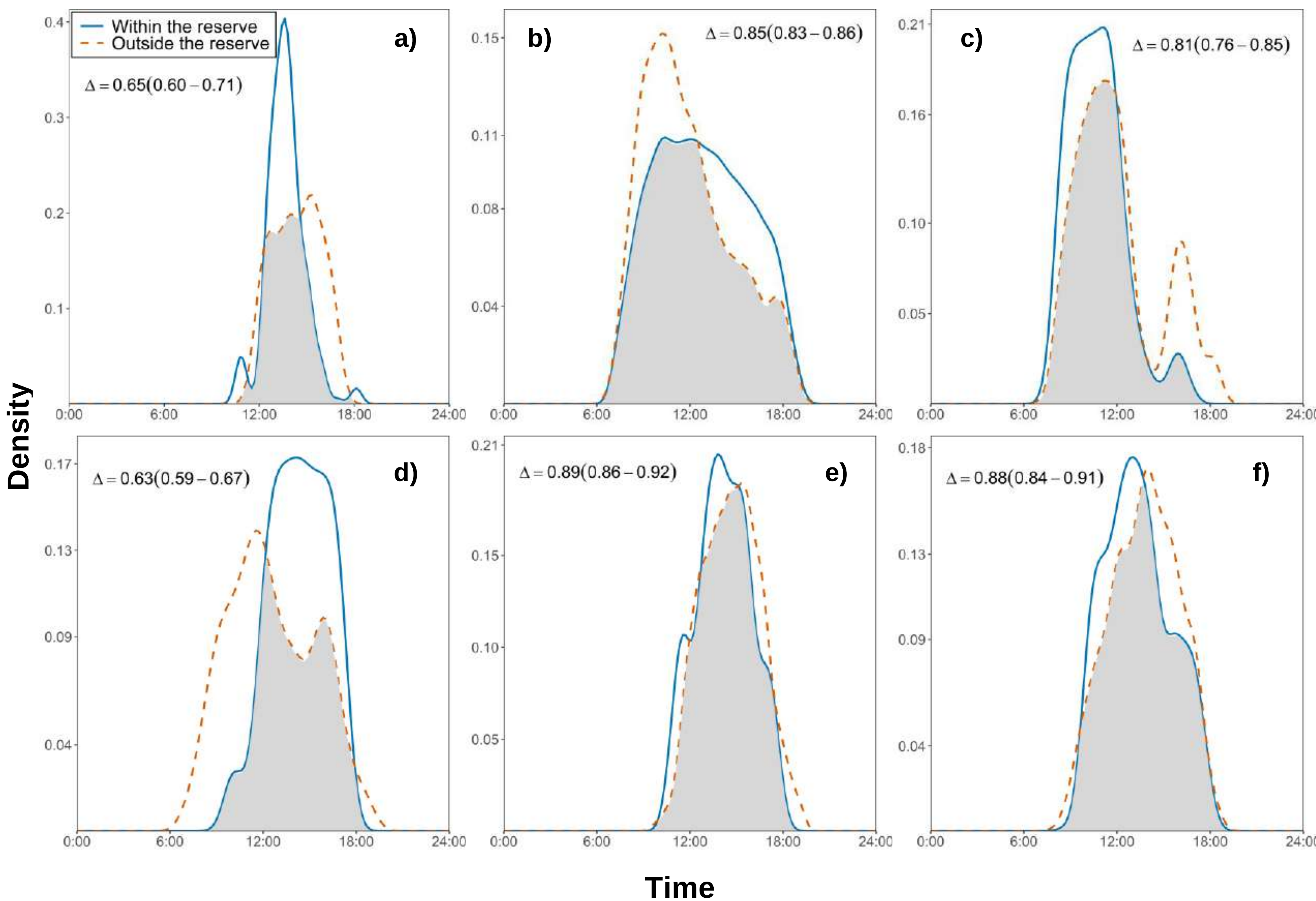
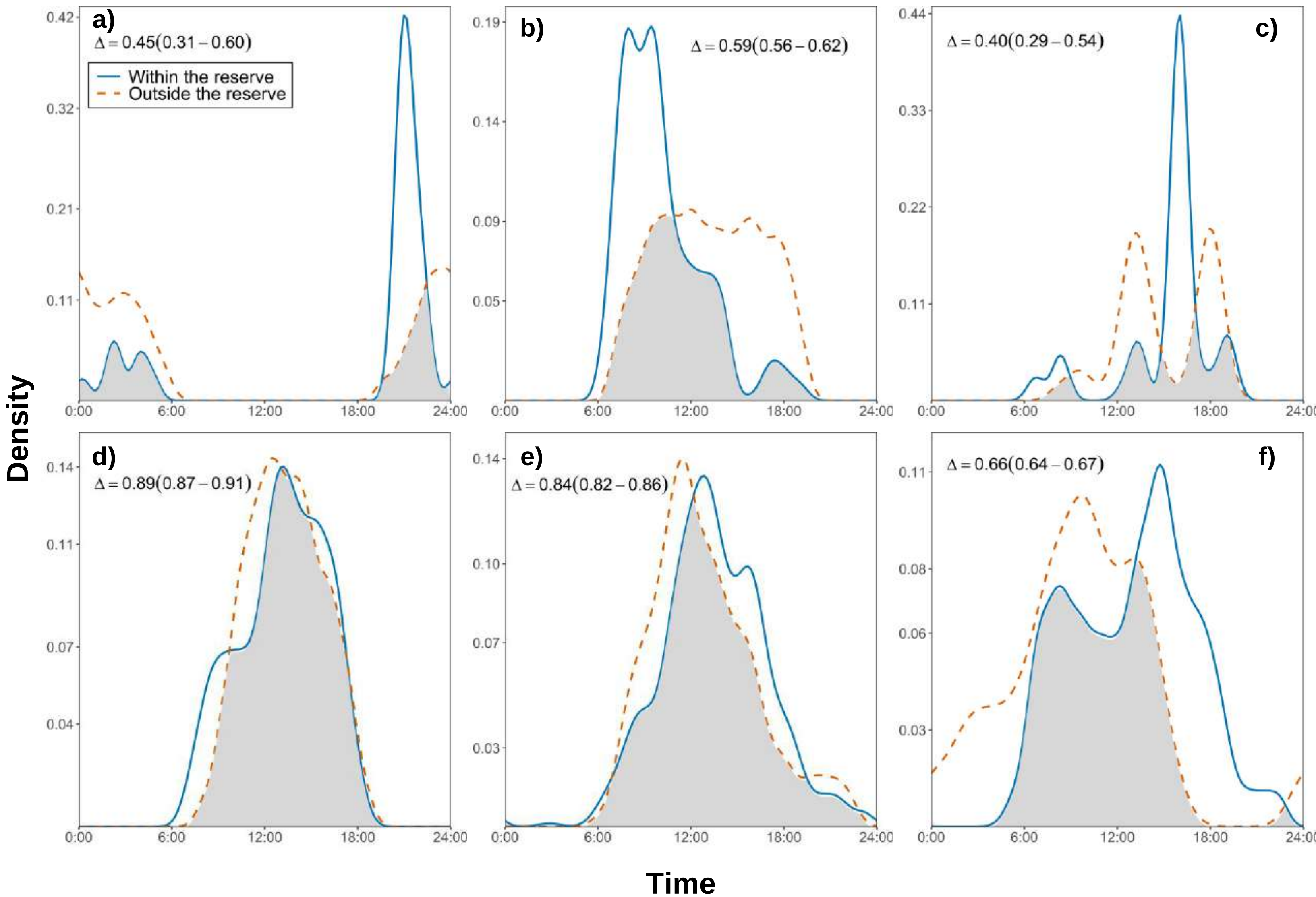


Figure S6. Comparison of daily activity patterns of *sartenejas* use within and outside the Calakmul Biosphere Reserve of a) *B. urubitinga*, b) *C. rubra*, c) *M. semitorquatus,* d) *O. vetula*, e) *P. morio* and f) *R. magnirostris*. Overlap coefficients with their 0.95% confidence intervals are shown in each case. Gray-shaded areas indicate overlap in activity.

1



2 **Figure S7.** Comparison of daily activity patterns of *sartenejas* use within and outside the Calakmul Biosphere Reserve: a) *C. paca*, b) *D. punctata*, c) *E. barbara*, d) *N. narica*, e) *P. tajacu* and f) *U. cinereoargenteus*. Overlap coefficients with their 0.95% confidence intervals are shown in each case. Gray-shaded areas indicate overlap in activity.

DISCUSIÓN Y CONCLUSIONES

Los resultados de este estudio amplían el conocimiento sobre la importancia ecológica de las sartenejas en la región de Calakmul, con lo cual se consolida la idea de que tanto aguadas como las sartenejas son sitios de alta relevancia ecológica para los vertebrados de la región de Calakmul. Asimismo, permiten poner en evidencia que la presencia humana y las distintas actividades productivas llevadas a cabo fuera de la Reserva de la Biosfera de Calakmul (CBR) están generando impactos sobre esta fauna que son diferenciales entre aves y mamíferos y que se pueden manifestar de forma sutil como los cambios en los patrones de uso de las sartenejas a lo largo del día.

Si bien se obtuvo información sumamente valiosa sobre cómo la fauna usa el agua contenida en las sartenejas en sitios con actividades humanas contrastantes en la región de Calakmul, existe aún una amplia variedad de posibilidades de estudios relacionados con estos cuerpos de agua. Por ejemplo, durante el trabajo en campo se observó a distintas especies de invertebrados en la materia orgánica acumulada en las sartenejas y en la revisión de los videos generados por las cámaras trampa se observó en múltiples ocasiones cómo individuos de *Crax rubra* rascaban y picaban esta materia orgánica, por lo que es posible que además de ser usadas como una fuente de agua las sartenejas sean sitios de forrajeo (Verdonschot, 2015).

Además, es necesario determinar si las características físicas contrastantes entre aguadas y sartenejas influyen en que estos cuerpos de agua tengan diferentes roles ecológicos para la fauna. Por ejemplo, la mayoría de las aguadas tiene una extensión mayor a 10 m^2, pero menor a media hectárea, mientras que las sartenejas generalmente no cubren más de un metro cuadrado (Reyna-Hurtado et al., 2012; Delgado-Martínez et al., 2018). Asimismo, mientras que se ha calculado una densidad de una aguada por cada 10.5 km^2 (Reyna-Hurtado et al., 2012) se estima que hay una sarteneja por cada 0.1 km^2 (datos no publicados). Además, las aguadas suelen encontrarse en depresiones topográficas con suelos arcillosos mientras que las sartenejas están presentes principalmente en sitios con roca madre expuesta (García-Gil et al., 2002; obs. pers.). De la misma manera, su hidroperiodo difiere, en el caso de las aguadas, algunas pueden almacenar agua durante todo el año, pero cuando se secan es necesaria una gran cantidad de lluvia para que recuperen su nivel. En contraste, la mayoría de las sartenejas se vacían durante la temporada de secas, pero pueden recuperar su nivel con un solo evento de lluvia de intensidad moderada (Reyna-Hurtado et al., 2012; Delgado-Martínez, pers. obs).

El mayor tamaño y disponibilidad del agua en las aguadas seguramente favorece el establecimiento de poblaciones de peces, reptiles y anfibios, que a su vez favorece a que distintas especies de aves puedan usarlas como sitios de forrajeo (Vega-Cendejas, 2002; Puc-Cabrera, 2008; Reyna-Hurtado et al., 2010), sin embargo, durante las actividades de campo de esta investigación se observó una puesta del orden Anura y a algunos individuos del orden Testudines en las sartenejas, por lo que las sartenejas también pueden ser un recurso de gran valor para otros organismos como es el caso de anfibios y reptiles (Flores, 1983). Asimismo, debido a su tamaño, las aguadas sirven para que animales de talla corporal grande como el jaguar, tapir y los pecaríes tomen "baños" que les pueden permitir regular su temperatura corporal y reducir su carga de ectoparásitos (Cain et al., 2006; Reyna-Hurtado et al., 2010; Moreira-Ramírez et al., 2016). Sólo en algunos casos, las sartenejas pueden tener la profundidad y extensión suficiente para que un grupo de pecaríes o un tapir entre completamente en ellas (obs. pers.), pero otras especies de menor tamaño (e.g., *Rupornis magnirostris*, *Ciccaba virgata*, *Pecari tajacu* y *Eira barbara*) las utilizaron frecuentemente para tomar baños, por lo que es importante conocer en qué medida este comportamiento ayuda a aves y mamíferos a regular su temperatura corporal y reducir su carga de ectoparásitos (Cain et al., 2006; Clayton et al., 2010; Mole et al., 2016; Bush y Clayton, 2018).

Un punto importante que es necesario clarificar es si, el constante uso de las aguadas por los humanos, en los ejidos, está interfiriendo con el uso de estos cuerpos de agua por la fauna silvestre, obligándola a usar fuentes de agua más pequeñas como las sartenejas (Crosmary et al., 2012). Esta posibilidad adquiere mayor relevancia si se toma en cuenta que, aunque la ganadería no es una de las principales actividades productivas en la región de Calakmul, cada vez es más común encontrar desmontes dedicados a la producción bovina y ovina donde las aguadas son usadas por el ganado, lo que puede agudizar el conflicto humano-fauna silvestre en la región (Amador-Alcalá et al., 2013; Ellis et al., 2017). Por último, es necesario conocer a detalle la distribución espacial y temporal (hidroperiodo) de las sartenejas, lo que a su vez nos permitiría conocer su papel en la conectividad del hábitat; en este sentido, puesto que las sartenejas acumulan agua incluso con lluvias moderadas, es posible que la fauna haga uso de ellas para reducir su déficit de agua (e.g., *stepping stones*) cuando se mueve entre aguadas o sitios de forrajeo distantes (Tulbure et al., 2014).

Tomando en cuenta la actual tendencia ambiental, hacia una fuerte degradación de los ecosistemas naturales, así como al cambio climático y los planes de desarrollo turístico para la región (i.e., proyecto del Tren Maya), es imprescindible generar un sistema de monitoreo biológico que nos permita detectar cambios en las comunidades de fauna silvestre y en los recursos limitantes como el agua. La incorporación de las sartenejas en el monitoreo biológico en la región de Calakmul es imprescindible y se justifica por dos motivos: 1) son sitios donde se concentra la actividad de un diverso conjunto de especies de aves y mamíferos que incluye a aquellas tan pequeñas como *Ceratopipra mentalis* y tan grandes como *Tapirus bairdii* y 2) proporcionan un recurso limitante en un área reducida que permite que la mayoría de las sartenejas pueden ser monitoreadas en su totalidad con una sola cámara trampa. La relevancia de las sartenejas como sitios ideales para el monitoreo biológico se ejemplifica en el registro *de Tayassu pecari* en una de las sartenejas dentro de la RBC siendo que esta especie no fue registrada en las aguadas monitoreadas por la Comisión Nacional de Áreas Naturales Protegidas (CONANP) y el equipo de trabajo de Reyna-Hurtado (Reyna-Hurtado com. pers.; Sima com. pers.) en esta misma área y durante el mismo periodo de estudio.

En los últimos años se ha observado una disminución de la precipitación en la Península de Yucatán y una modificación en los patrones de lluvia en la región de Calakmul, la cual se caracteriza por lluvias más intensas pero distribuidas de manera heterogénea a lo largo del año (Mardero et al., 2012, 2020). Esto ha propiciado una tendencia de desecación de las aguadas durante los últimos años en la región de Calakmul (O'Farril et al., 2014; Reyna-Hurtado et al., 2019). Ante esta situación, la CONANP ha decidido colocar bebederos artificiales dentro de la RBC, en los que se ha registrado la visita de al menos 20 especies (CONANP, 2019). Una alternativa a esta estrategia sería abastecer con agua algunas sartenejas para usarlas con el mismo fin (durante el muestreo dentro de la RBC, se ubicaron algunas sartenejas que se encuentran a menos de 100 m de la carretera que conduce a las ruinas de Calakmul). En ambos casos se debe proceder con cautela y un constante monitoreo de los resultados, sin embargo, al abastecer con agua a las sartenejas se estaría aprovechando una característica natural del ecosistema lo cual a su vez podría disminuir los posibles efectos negativos que se han registrado al proporcionar agua a la fauna silvestre, tales como modificaciones en sus patrones de movimiento y patrones de forrajeo (Smit et al., 2007; Simpson et al., 2011; Purdon y van Aarde, 2017).

Finalmente, los resultados de este proyecto permiten concluir que, aunque la región de Calakmul cuenta con una cubierta forestal relativamente extensa y poco fragmentada, las actividades humanas que se realizan fuera de la RBC tienen un impacto negativo en el uso que hacen aves y mamíferos de un recurso clave para el mantenimiento de la biodiversidad. Dicho impacto se manifiesta en la modificación de la composición de los ensamblajes y comportamiento de las especies de aves y mamíferos que hacen uso del agua contenida en las sartenejas; por lo tanto, es indispensable desarrollar estrategias que permitan mitigar el efecto del disturbio antropogénico fuera de la RBC. Asimismo, se puede concluir que debido al recurso que proporcionan las sartenejas en un área tan reducida, el monitoreo de estos cuerpos de agua permite registrar a un alto porcentaje de las especies presentes en la región y su respuesta a las actividades humana; de tal modo que es altamente deseable incorporar a estos cuerpos de agua al monitoreo biológico tanto dentro como fuera de la RBC.

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