*Journal of Tropical Ecology*

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**Research Article**

**Cite this article:** Delgado-Martínez CM, Alvarado F, Kolb M, and Mendoza E (2022) Monitoring of small rock pools reveals differential effects of chronic anthropogenic disturbance on birds and mammals in the Calakmul region, southern Mexico. *Journal of Tropical Ecology* **38**, 79–88. https://doi.org/10.1017/S0266467421000547

Received: 7 October 2020
Accepted: 26 November 2021
First published online: 17 December 2021

**Keywords:**
camera trapping; protected areas; tropical forest; water bodies; wildlife monitoring; Selva Maya

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# Monitoring of small rock pools reveals differential effects of chronic anthropogenic disturbance on birds and mammals in the Calakmul region, southern Mexico

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## Abstract

Great attention has been drawn to the impacts of habitat deforestation and fragmentation on wildlife species richness. In contrast, much less attention has been paid to assessing the impacts of chronic anthropogenic disturbance on wildlife species composition and behaviour. We focused on natural small rock pools (*sartenejas*), which concentrate vertebrate activity due to habitat's water limitation, to assess the impact of chronic anthropogenic disturbance on the species richness, diversity, composition, and behaviour of medium and large-sized birds and mammals in the highly biodiverse forests of Calakmul, southern Mexico. Camera trapping records of fauna using *sartenejas* within and outside the Calakmul Biosphere Reserve (CBR) showed that there were no effects on species richness, but contrasts emerged when comparing species diversity, composition, and behaviour. These effects differed between birds and mammals and between species: (1) bird diversity was greater outside the CBR, but mammal diversity was greater within and (2) the daily activity patterns of birds differed slightly within and outside the CBR but strongly contrasted in mammals. Our study highlights that even in areas supporting extensive forest cover, small-scale chronic anthropogenic disturbances can have pervasive negative effects on wildlife and that these effects contrast between animal groups.

## Introduction

Anthropogenic activities are exerting unprecedented pressure on tropical wildlife, threatening the extinction of a large proportion of its species in the coming years (Hoffmann et al. 2010, IPBES 2019, Venter et al. 2016). This situation creates an urgent need for detailed data to understand the nature of human impact and provide the foundations to implement specific initiatives to mitigate its effects at regional and local scales (Bull et al. 2014, Kindsvater et al. 2018). Yet, regardless of the considerable effort that has been made to assess the impacts of anthropogenic activities on tropical wildlife, important knowledge gaps remain due to conceptual and methodological issues.

Current studies emphasise the impacts of drastic habitat transformations such as extensive deforestation and fragmentation on faunal diversity (Alroy 2017, Gibson et al. 2011, Maxwell et al. 2016). In comparison, less attention has been paid to assessing the negative effects that more subtle but chronic anthropogenic disturbances (e.g. subsistence hunting, anthropogenic noise, and selective logging) have on ecological features such as species composition and behaviour, in sites where forest cover is still relatively extensive (Gonçalves et al. 2020, Singh 1998). Moreover, studies usually focus on a reduced subset of species assuming that responses to perturbations are similar for those species not evaluated (Carmel et al. 2013). Focusing on small subsets of species can lead to important biases in the understanding of the overall responses of vertebrates to human perturbation and, therefore, in the design of effective conservation strategies for maintaining faunal diversity. Thus, having animal surveys that include a large proportion of the local fauna are highly desirable. Unfortunately, some wild vertebrates are recorded in such low frequencies, even when using modern technologies, such as camera traps, that the possibilities of detecting impacts of human perturbation are greatly limited (Kays et al. 2020, Kelly 2008).

Small natural features (i.e. sites with ecological importance that is disproportionate to their size, Hunter 2017), such as fruiting trees, mineral licks, and water bodies, attract a great variety of wildlife species and provide the opportunity to simultaneously record information on animal diversity, composition, abundance, and behaviour even for rare species (e.g. Camargo-Sanabria & Mendoza 2016, Matsubayashi et al. 2007, Vale et al. 2015). An additional advantage is that the study of small natural features can provide evidence about the use that different species make of key resources. Hence, there is great potential for monitoring efforts focused on such natural features to increase our understanding of the impacts that anthropogenic activities have on a broader variety of wildlife species (e.g. Blake et al. 2013, Eaton et al. 2017).

Tropical forests growing on karst in the Calakmul region (southern Mexico) stand out at the global level due to their importance as biodiversity strongholds, but also due to their increased level of threat (Myers et al. 2000). In these forests, most of the rainfall infiltrates underground provoking a lack of surface rivers and extensive permanent water bodies (García-Gil et al. 2002). Nonetheless, free-standing water is available in water bodies locally known as *aguadas* and *sartenejas*. *Aguadas*, known as dolines in geological terms (Allaby 2020), are natural shallow depressions that have soils with a high clay content where water from precipitation and seasonal streams is collected and stored (Fig. S1a-b; García-Gil et al. 2002, Torrescano-Valle & Folan 2015). These water holes occur at an approximate density of one per 10.5 km$^2$ most of them covering less than a half hectare (Reyna-Hurtado et al. 2012). Depending on their hydroperiod, the *aguadas* can be intermittent (if they dry up after several months) or semipermanent (if they dry only occasionally during severe droughts) (Colburn 2008). On the other hand, *sartenejas* (kamenitzas in geological terms; Allaby 2020) are small rock pools created in crevices opened in exposed bedrock where rainfall accumulates (Fig. S1c, d; Flores 1983). There is approximately one *sarteneja* per 0.1 km$^2$, and they usually cover less than a square meter (Delgado-Martínez et al. unpubl. data). *Sartenejas* can collect water even during light rainfall events (Reyna-Hurtado et al. 2012) exhibiting short hydroperiods (a few weeks). Both water sources are heavily exploited by a highly diverse fauna (Delgado-Martínez et al. 2018, Reyna-Hurtado et al. 2009, 2010). The Calakmul region has recently experienced an increase in the frequency of droughts and disruptions in its rainfall patterns (i.e. rainfall more unevenly distributed, Mardero et al. 2012, 2020) causing several of the *aguadas* to more frequently dry up (Reyna-Hurtado et al. 2019). Because of this, the importance of *sartenejas* as a water source for wildlife would likely increase. Moreover, due to their small size, it is easier to monitor *sartenejas* than *aguadas* (Delgado-Martínez et al. 2018) which makes them ideal for assessing human impact over a wide variety of vertebrate species.

Here, we use *sartenejas* to assess the combined impacts of small-scale frequent human activities (i.e. beekeeping, hunting, subsistence farming, selective logging, and vehicle transit) on species diversity, composition, and behaviour of medium- and large-sized birds (> 170 g) and terrestrial mammals (> 450 g) in the highly biodiverse forests of Calakmul. By comparing the use of *sartenejas* within and outside the Calakmul Biosphere Reserve (CBR), we expect to detect differences in species diversity and composition of bird and mammal assemblages reflecting the loss (or reduction in abundance) of species sensitive to anthropogenic disturbance and the spread of alien fauna (e.g. cattle and dogs) (Dornelas et al. 2014, Newbold et al. 2018, Vetter et al. 2011). Moreover, we expect that birds and mammals will modify the duration of their visits and their daily activity patterns outside the CBR as an adjustment to avoid humans (Gaynor et al. 2018, Suraci et al. 2019). Since different studies have found that birds and mammals differ in their response to anthropogenic disturbance (e.g. Benítez-López et al. 2010, Fontúrbel et al. 2015, Sauvajot et al. 1998), we expect the magnitude of the above-mentioned effects to differ between these two groups.

## Methods

### Study area

Fieldwork was conducted in the southern portion of the CBR and in the 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 covers 2,000,000 ha and is part of the Mesoamerican Biological Corridor and the Selva Maya, constituting the second largest tract of tropical forest in the Americas (Galindo-Leal 1999). Despite maintaining an extensive forest cover, this region is undergoing an increase in activities such as selective logging, hunting, farming, and cattle ranching (Calmé & Guerra 2005, Ramírez-Delgado et al. 2014). The climate in this region is tropical and subhumid, with a dry season lasting from November to April and a rainy season lasting from May to October (Vidal-Zepeda 2005). The mean annual precipitation of the region is 1,059 mm, but annual precipitation has ranged from 340 to 1,527 mm over the last 30 years (CONAGUA 2020). In the last 10 years, the Calakmul region has experienced an increase in drought frequency and changes in its precipitation regime which have caused the occurrence of very dry years but also very intense rainfall events (Mardero et al. 2012, 2020). The CBR was established in 1989 and has a total extent of 723,185 ha (Gómez-Pompa & Dirzo 1995). At both national and global levels, this reserve is one of the last strongholds for several endangered species, such as the bird *Meleagris ocellata* and the mammals *Tapirus bairdii* and *Tayassu pecari* (Kampichler et al. 2010, Naranjo et al. 2015). Human activities in the CBR study site are restricted to ecotourism and biological and archeological research. The communal lands of the *Nuevo Conhuas* village cover 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). The *Nuevo Conhuas'* communal lands are the closest to our CBR study site (distance between polygon centroids = 35.36 km) and are similar to other communal lands located in the vicinity of the CBR in terms of the activities they develop and the characteristics of the forest cover (Calmé & Guerra 2005, Ramírez-Delgado et al. 2014). Different human activities, and with contrasting magnitude, occur in the CBR and *Nuevo Conhuas* (Table 1).

### *Selection and monitoring of* sartenejas

Our focal *sartenejas* were located in the southern portion of the CBR (hereafter "within the reserve") and in the communal lands of *Nuevo Conhuas* (hereafter "outside the reserve") (Fig. S2). We recorded the location of 20 *sartenejas* within the reserve, two of them were previously reported by Reyna-Hurtado et al. (2012), and 18 were located for this study with the help of local guides and by searching along 26 transects (total length = 116.6 km). From these *sartenejas,* we selected 10 to be monitored.

**Table 1.** Factors associated with anthropogenic disturbance in the areas where focal *sartenejas* were located in the Calakmul region (Campeche, southern Mexico).

| | | Within the reserve | Outside the reserve |
|---|---|---|---|
| Human settlements | | No | Yes |
| Human activities [a, b] | | Tourism, biological, and archaeological research | Cattle ranching, beekeeping, selective logging, subsistence farming, and hunting [e] |
| Years without primary sector activities | | 31 | None |
| Human activity hours | | 6 a.m. - 6 p.m. | Without restrictions |
| Guard presence | | Yes | No |
| Roads [c, d] | Vehicles transiting | Automobiles, trucks motorbikes | Automobiles, trailers, trucks, motorbikes, buses, bicycles, horses |
| | Average cars per day | 41 | 2242 |

[a] INE (1999).
[b] Calmé & Guerra (2005).
[c] SCT (2019).
[d] CONANP unpubl. data.
[e] People are usually accompanied by dogs during field activities (Andrés Barrientos pers. comm.).

Moreover, we selected 9 *sartenejas* outside the reserve based on information provided by local guides. To select the *sartenejas* to be monitored, we used the following criteria: 1) to have a volume $\geq$ of 20 L and 2) to be located $\geq$ 1 km from any other monitored *sarteneja*. The average (± SD) distance between *sartenejas* was 7.48 ± 4.36 km and 6.81 ± 3.12 km within and outside the reserve, respectively. We used GPS tracks generated during our travels on the roads and georeferenced points to calculate the distance from *sartenejas* to the closest road and the site with permanent human presence (hereafter "SWIPHs", see Appendix S1). Additionally, we used the vegetation cover map provided by the Monitoring Activity Data for the Mexican REDD+ program which is based on Sentinel-2 imagery for the year 2018 (CONABIO 2021) to: (1) calculate the distance from *sartenejas* to the closest farmland outside the reserve, (2) obtain the vegetation type of the location of *sartenejas*, and (3) estimate the forest cover within a 1-km buffer around the *sartenejas*. Except for a *sarteneja* outside the reserve, which was in a lowland sub-perennial forest, all the *sartenejas* were in medium height sub-perennial forest. The average (± SD) forest cover within a 1-km buffer around the *sartenejas* was 99.99 ± 0.02% and 95.45 ± 4.37% within and outside the reserve, respectively. There were no significant differences in canopy cover ($W = 22$, $p = 0.221$), mean monthly temperature ($t = 0.751$, $p = 0.457$), maximum monthly temperature ($t = 1.855$, $p = 0.071$), minimum monthly temperature ($t = -1.443$, $p = 0.157$), nor monthly rainfall ($t = 0.022$, $p = 0.983$) between *sartenejas* located within and outside the reserve during the study period (Appendix S1).

We set up one camera trap (models Browning Strike Force Elite BTC5HDE, Bushnell Trophy Cam HD Aggressor 119876C, and Stealth Cam G42NG triggered by motion) aimed at each *sarteneja* and programmed to take a 20-s long video each time it was activated and to have a 5-s resting time before reactivation. In most of the cases (ca. 90%), the camera trap monitored the whole extent of the *sarteneja*. The monitoring was conducted over one year (April 2018 to March 2019) to include the dry and wet seasons.

### Data analysis

We identified all the mammal and bird species that used the water contained in the *sartenejas*. We only discarded records of *Ateles geoffroyi*, an arboreal species whose activities mostly occur in the canopy beyond the detection area of our camera traps. To prevent counting each video of the same species as a different visitation, we grouped records following the procedure described in Camargo-Sanabria & Mendoza (2016). This approach allows calculating a species-specific minimum time to group consecutive videos of the same species and camera by plotting the number of groups of videos that emerge using increasing intervals of time (from 1 to 1440 minutes). The time interval that is selected to group videos corresponds to the moment the number of groups of videos reaches stability. Therefore, an event corresponds to a single record or grouped records. We calculated the frequency of use of *sartenejas* for each species using the following equation: (number of events/sampling effort) × 1,000 camera days (O'Brien et al. 2003). To estimate the duration of use of *sartenejas*, we calculated the difference between the end and the beginning of an event.

### *Diversity and composition of animal assemblages using* sartenejas *within and outside the reserve*

We estimated the sample coverage of birds and mammals in each site by conducting an individual-based sampling coverage analysis (Chao & Jost 2012). Individual sample-based rarefaction and extrapolation curves of Hill numbers ($q = 0, 1,$ and $2$) and the corresponding 95% confidence intervals were generated to compare bird and mammal diversity within and outside the reserve (Chao et al. 2014). These analyses were conducted using the *iNEXT* R package (Hsieh et al. 2020) and were restricted to assemblages constituted by 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 frequencies of use of *sartenejas*). We performed an analysis of similarities (ANOSIM) to test for the existence of statistical differences in species composition between assemblages. For this analysis, we included both native and non-native species and used the *vegan* R package (Oksanen et al. 2019).

To assess how distance to roads and SWIPHs related to the composition of bird and mammal assemblages, we conducted a redundancy analysis (RDA) on a Bray–Curtis distance matrix (calculated based on frequencies of use of *sartenejas*) using predictors standardised to zero mean and unit variance. We did not include the distance to farmlands outside the reserve because it was highly correlated with the distance to roads ($R = 0.63$, $p < 0.05$). We tested the significance of the entire model and each of its terms using a PERMANOVA test with 1,000 permutations. For these analyses, we included those species that were recorded in at least half of the sites and used the *vegan* R package (Oksanen et al. 2019).

### *Patterns of use of* sartenejas *by birds and mammals within and outside the reserve*

To compare the frequency and duration 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 of use ($\hat{d}_u$) and duration of visitation ($\hat{d}_l$) within and outside the reserve for each recorded vertebrate species. Second, we generated a null distribution of mean differences based on 10,000 permutations. In cases where the observed differences were 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); when the observed differences were 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 of mean differences using 10,000 bootstrap samples. We restricted this analysis to those species recorded in at least two *sartenejas* in each site.

We compared daily activity patterns of use of *sartenejas* in species that had at least 10 events in each site by applying the Ridout & Linkie (2009) method. Following Meredith & Ridout (2018), we estimated the activity overlap between events within and outside the reserve using the estimator of the coefficient of overlapping $\Delta_1$ for small samples (less than 75 observations) and $\Delta_4$ for larger samples (more than 75 observations). We used the *basic0* method for the calculation of 95% confidence intervals. We calculated overlap coefficients and confidence intervals using the *overlap* R package (Ridout & Linkie 2009). Finally, we used a randomisation test that generates a null distribution of overlap indices using 1,000 bootstrap samples, this randomised distribution was used to estimate the probability ($p$-value) that the observed overlap arose by chance (Rowcliffe 2021).

## Results

We accumulated 4,646 camera trap days of sampling, 2,309 within the reserve, and 2,337 outside the reserve. Camera traps generated a total of 35,369 videos with at least one animal visible, it was not possible to identify the species in less than 1% of the cases. We identified a total of 46 species (21 bird and 25 mammal species; Tables S1) using the *sartenejas*: 16 bird and 20 mammal species within the reserve and 16 bird and 22 mammal species outside the reserve. Overall, the most common species using the *sartenejas* were the bird *Crax rubra* and the mammal *Dasyprocta punctata*.

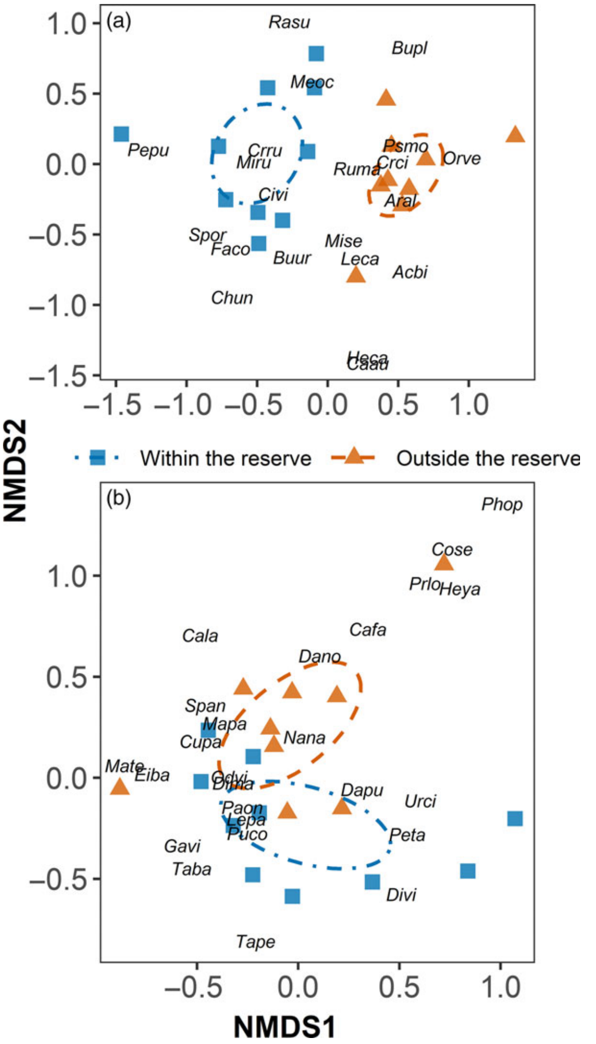

**Figure 1.** Variation in the species composition of (a) bird and (b) mammal assemblages using *sartenejas* within and outside the Calakmul Biosphere Reserve, Campeche, southern Mexico. Ellipses represent 95% confidence intervals. Bird species codes: *Acbi* = *A. bicolor*, *Aral* = *A. albiventris*, *Bupl* = *B. plagiatus*, *Buur* = *B. urubitinga*, *Caau* = *C. aura*, *Chun* = *C. uncinatus*, *Civi* = *C. virgata*, *Crru* = *C. rubra*, *Crci* = *C. cinnamomeus*, *Faco* = *F. columbarius*, *Heca* = *H. cachinnans*, *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: *Cafa* = *C. lupus familiaris*, *Cala* = *C. latrans*, *Cose* = *C. semistriatus*, *Cupa* = *C. paca*, *Dapu* = *D. punctata*, *Dano* = *D. novemcinctus*, *Dima* = *D. marsupialis*, *Divi* = *D. virginiana*, *Eiba* = *E. barbara*, *Gavi* = *G. vittata*, *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*.

### *Diversity and composition of animal assemblages using* sartenejas *within and outside the reserve*

Sample coverage of the bird survey was estimated at 99% both within and outside the reserve (Table S2). The 95% confidence intervals of individual-based sample interpolation and extrapolation curves for bird species richness (q = 0) overlapped, suggesting that there was no significant difference in the species richness of the assemblages using the *sartenejas* within and outside the reserve (Fig. S3). However, the comparison of Shannon and Simpson diversity curves for bird species (q = 1 and 2, respectively) showed that diversity was significantly higher outside than within the reserve (Fig. S3). The observed bird species richness within and outside the reserve was only slightly lower than estimated: 16 vs. 16.25 ± 0.73 and 16 vs. 17 ± 3.74 (mean ± SE). Bird assemblages using the *sartenejas* within and outside the reserve were statistically different (ANOSIM; $R = 0.69$, $p < 0.001$, Fig. 1a). The bird species *Chondrohierax uncinatus*, *Falco columbarius*, *Penelope purpurascens*, and *Spizaetus ornatus* were recorded exclusively within the reserve, while *Accipiter bicolor*, *Aramides albiventris*, *Buteo* *plagiatus*, *Cathartes aura,* and *Herpetotheres cachinnans* were recorded only outside the reserve. Differences in bird assemblages using the *sartenejas* were significantly related to distances to roads and SWIPHs (RDA; $F = 2.80$, $p < 0.01$, Fig. S4a). Distance to roads ($F = 5.29$, $p < 0.001$) was positively related to the frequency of use by *C. rubra* both within and outside the reserve, whereas it was negatively related to the frequency of use by *Ortalis vetula*, *Psilorhinus morio,* and *Rupornis magnirostris* outside the reserve. Distance to SWIPHs ($F = 2.36$, $p < 0.05$) was negatively related to the frequency of use by *Micrastur semitorquatus* both within and outside the reserve.

In the case of mammals, sample coverage was estimated at 99% within the reserve and 100% outside the reserve (Table S2). As with birds, the 95% confidence intervals of individual-based sample interpolation and extrapolation curves for mammal species richness overlapped indicating that richness was similar within and outside the reserve (Fig. S3). In contrast with birds, Shannon and Simpson diversity curves showed that diversity was higher within than outside the reserve (Fig. S3). The observed mammal richness within the reserve was lower than the estimated (20 vs. 27.98 ± 11.64), but outside the observed richness was the same as the estimated (20 vs. 20 ±0.65). Differences in the composition of mammals using the *sartenejas* within and outside the reserve were lower than in the case of birds, though still statistically significant (ANOSIM; $R = 0.25$, $p < 0.01$, Fig. 1b). The species *Galictis vittata*, *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. Differences in mammal assemblages using the *sartenejas* were significantly related to distances to roads and SWIPHs (RDA; $F = 1.68$, $p < 0.01$, Fig. S4b). Distance to roads ($F = 2.27$, $p < 0.01$) was positively related to the frequency of use by *Leopardus pardalis* both within and outside the reserve and to the frequency of use by *Panthera onca* within the reserve; in contrast, the frequency of use by *Nasua narica* was negatively related to distance to roads both within and outside the reserve and the frequency of use by *Cuniculus paca* and *D. punctata* outside the reserve. Distance to SWIPHs ($F = 1.81$, $p < 0.05$) was positively related to the frequency of use by *Puma concolor* and *Urocyon cinereoargenteus* outside the reserve.

### *Patterns of use of* sartenejas *by birds and mammals within and outside the reserve*

The three bird species most frequently recorded using the *sartenejas* within the reserve were, in descending order, *C. rubra* (65.08% of bird records within the reserve), *P. morio* (6.35%), and *R. magnirostris* (5.71%). In comparison, outside the reserve, the corresponding species were *P. morio* (44.95%), *R. magnirostris* (16.64%), and *O. vetula* (11.82%) (Fig. S5a). The frequency of use of *sartenejas* by *C. rubra* decreased by 86% outside the reserve ($\hat{d}_u = 153.40$, $p < 0.001$) and the duration of its visits by 66% ($\hat{d}_l = 6168$, $p < 0.001$) (Fig. 2a and S6a). In contrast, the frequency of the use of *sartenejas* by *Crypturellus cinnamomeus*, *O. vetula, P. morio*, and *R. magnirostris* increased outside the reserve by seven ($\hat{d}_u = -5.86$, $p < 0.05$), twelve ($\hat{d}_u = -31.86$, $p < 0.001$), five ($\hat{d}_u = -98.60$, $p < 0.001$), and two times ($\hat{d}_u = -28.80$, $p < 0.05$), respectively (Fig. 2a). The remaining bird species (50% of the total number of evaluated species) showed no difference in their frequency of use of *sartenejas* or the duration of their visits within versus outside the reserve (Fig. 2a).

We found significant differences between daily activity patterns within and outside the reserve for the seven evaluated bird species, with overlap coefficients ranging between 0.64 and 0.90 (mean overlap ± SD = 0.77 ± 0.12; Fig. S7). The species *C. rubra* ($\Delta = 0.84$, 95% CI [0.82, 0.85], $p < 0.001$), *M. semitorquatus* ($\Delta = 0.87$, 95% CI [0.82, 0.92], $p < 0.001$), *P. morio* ($\Delta = 0.84$, 95% CI [0.82, 0.86], $p < 0.001$), and *R. magnirostris* ($\Delta = 0.90$, 95% CI [0.87, 0.93], $p < 0.001$) showed minor changes in their daily activity patterns (Fig. S7b, S7d and S7f-g). The most pronounced differences among birds occurred in *Buteogallus urubitinga* ($\Delta = 0.65$, 95% CI [0.60, 0.71], $p < 0.001$), *M. ocellata* ($\Delta = 0.66$, 95% CI [0.62, 0.71], $p < 0.001$), and *O. vetula* ($\Delta = 0.64$, 95% CI [0.60, 0.67], $p < 0.001$) (Fig. S7a, S7c, and S7e) which had different peaks of activity in the two sites.

Among mammals, the three most common users of *sartenejas* within the reserve were *Pecari tajacu* (21.99%), *N. narica* (11.81%), and *U. cinereoargenteus* (11.81%). Outside the reserve, *D. punctata* (23.94%), *N. narica* (23.07%), and *P. tajacu* (12.41%) were the three most common users (Fig. S5b). The frequency of use of *sartenejas* by *L. pardalis*, and *T. bairdii* decreased, respectively, by 82% ($\hat{d}_u = 16.07$, $p < 0.01$) and 92% ($\hat{d}_u = 9.39$, $p < 0.05$) outside the reserve (Fig. 2b). In contrast, *C. paca*, *D. punctata*, and *N. narica* increased their frequency of use of *sartenejas*, respectively, by ten ($\hat{d}_u = -21.38$, $p < 0.05$), three ($\hat{d}_u = -49.40$, $p < 0.05$), and two times ($\hat{d}_u = -40.80$, $p < 0.05$) outside the reserve (Fig. 2b). The rest of the evaluated mammal species (62%) showed no changes in their frequency of use of *sartenejas* (Fig. 2b). Only *C. paca*, *D. punctata,* and *N. narica* increased the duration of their visits to *sartenejas* outside the reserve by 12 ($\hat{d}_l = -1396$, $p < 0.05$), four ($\hat{d}_l = -3856$, $p < 0.01$), and two times ($\hat{d}_l = -2930$, $p < 0.05$), respectively (Fig. S6b).

The occurrence of differences in daily activity patterns within and outside the reserve was common among the 10 evaluated mammal species, with overlap coefficients ranging between 0.21 and 0.87 (mean overlap ± SD = 0.54 ± 0.23; Fig. 3 and S8). The daily activity patterns of *N. narica* ($\Delta = 0.87$, 95% CI [0.85, 0.89], $p < 0.001$) and *P. tajacu* ($\Delta = 0.87$, 95% CI [0.85, 0.89], $p < 0.001$) differed only slightly when compared within and outside the reserve (Fig. S8d-e). Species such as *Eira barbara* ($\Delta = 0.43$, 95% CI [0.31, 0.56], $p < 0.001$), *L. pardalis* ($\Delta = 0.55$, 95% CI [0.39, 0.72], $p < 0.001$), *Odocoileus virginianus* ($\Delta = 0.34$, 95% CI [0.25, 0.43], $p < 0.001$), and *U. cinereoargenteus* ($\Delta = 0.77$, 95% CI [0.75, 0.79], $p < 0.001$) were active within the same range of the day within and outside the reserve but the occurrence of their activity peaks differed (Fig. 3a, 3d, S8c and S8f). In comparison, *P. concolor* ($\Delta = 0.32$, 95% CI [0.28, 0.36], $p < 0.001$) and *M. pandora* ($\Delta = 0.21$, 95% CI [0.17, 0.24], $p < 0.001$) modified their activity from being mostly diurnal within the reserve to being more nocturnal outside the reserve (Fig. 3b-c). Finally, *C. paca* ($\Delta = 0.45$, 95% CI [0.30, 0.60], $p < 0.001$) and *D. punctata* ($\Delta = 0.59$, 95% CI [0.56, 0.62], $p < 0.001$) had marked peaks in activity time within the reserve, whereas outside their activity had not marked peaks (Fig. S8a-b).

## Discussion

Our monitoring focused on *sartenejas* was successful in terms of allowing us to record a very high proportion of the local fauna in our target groups. For example, the mammal species recorded accounted for 100% (23 out of 23) of the medium- and large-sized terrestrial mammals listed for the Calakmul region (INE 1999). This provided us with a strong foundation to explore the response

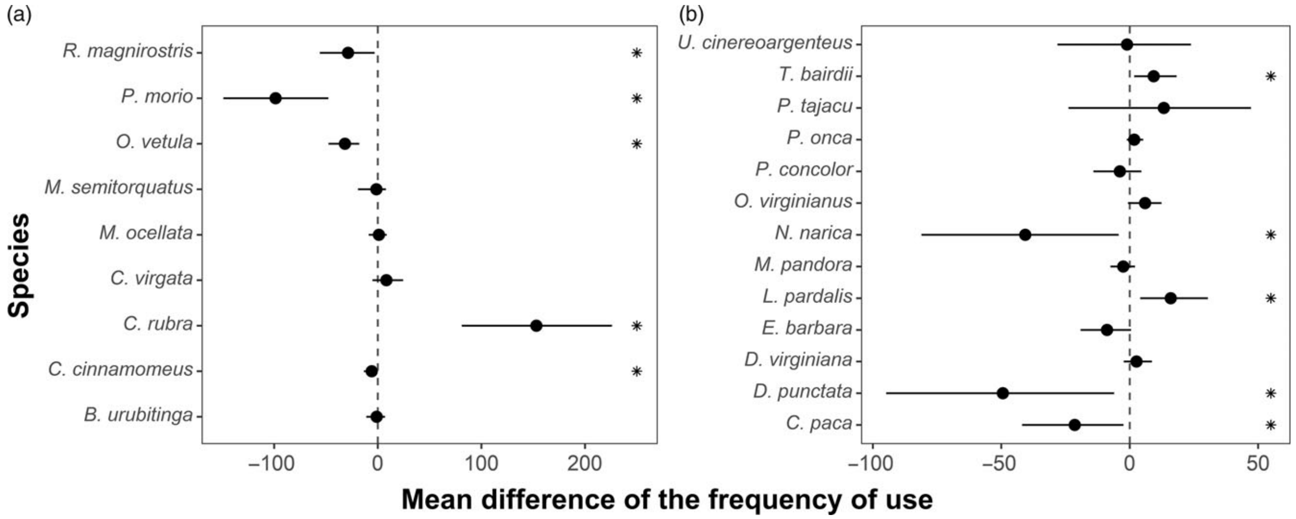

**Figure 2.** Differences in the frequency of use of *sartenejas* by (a) birds and (b) mammals within and outside the Calakmul Biosphere Reserve, Campeche, southern Mexico. Dots and bars represent the species mean differences in frequencies of visitation and the corresponding 95% bootstrap confidence intervals. Values located to the left of the dotted line represent a higher frequency of use of *sartenejas* outside the reserve and those located to the right represent higher frequencies within the reserve. Statistical differences ($p$-value < 0.05) are indicated with an asterisk.

of species to the effect of small scale but frequent human activities in a region that still maintains an extensive forest cover. We confirmed some of the most evident impacts human activity has already had on the wildlife outside the reserve (e.g. absence of some native species and increased presence of non-native species). But we also detected some incipient effects (e.g. changes in daily activity patterns) that might constitute an early warning of the increased influence of human activity on local wildlife populations. Our methodological approach contrasts with those used in several studies, which concentrate on a single species or small subsets of species and attempt to generalise to the overall target community.

We did not detect an impact at the level of species richness, one of the most commonly used parameters to assess the anthropogenic impact on animal communities (Gibson et al. 2011). However, as we shifted the focus of our attention from species richness to assemblage diversity, composition, and species behaviour, we started to find signs of anthropogenic impact. Therefore, it appears that by heavily focusing on species richness, studies risk underestimating the pervasiveness of chronic anthropogenic disturbances on wildlife, particularly in areas where natural vegetation is still extensive as in the Calakmul region (Dornelas et al. 2014, Fleishman et al. 2006, Newbold et al. 2018, Ramírez-Delgado et al. 2014).

Despite occurring at a relatively low intensity, human activities outside the reserve appear to be unleashing a series of effects that are directly impacting wildlife by changing the balance of factors that determine their occurrence and activity. The most obvious factor that can have a direct negative impact on some of the species is hunting. Large terrestrial birds and mammals, such as *C. rubra* and *Mazama* spp., are among the most hunted species in the Calakmul region (Calmé & Guerra 2005, Escamilla et al. 2000). This would help to explain the absence of these species or their reduced activity in the *sartenejas* outside the reserve. Abundances of bird and mammal species that are hunted for wild meat consumption or persecuted due to conflicts with livestock (i.e. large carnivores) decline with proximity to roads and settlements (Benítez-López et al. 2017). This is in agreement with our finding that the distance to roads or SWIPHs was positively associated with the frequency of use of *sartenejas* (i.e. the greater the distance the higher frequency of use) by the species *C. rubra*, *L. pardalis, P. concolor*, and *U. cinereoargenteus* outside the reserve. Therefore, the lower frequency of use that we detected outside the reserve for some species might be directly related to their local densities in sites with hunting pressure (Briceño-Méndez et al. 2016, Reyna-Hurtado & Tanner 2007).

Alternatively to hunting pressure, a series of more complex effects brought about by human presence are those related to the potential generation of a new landscape of fear (i.e. how animals perceive the trade-off between the use they require to do of essential resources and their safety) (Clinchy et al. 2016, Darimont et al. 2015, Suraci et al. 2019). Human activities outside the reserve which are more intense near roads and the village, even when not lethal for fauna, can deter visitation by sensitive species (e.g. Briceño-Méndez et al. 2016, Sánchez-Pinzón et al. 2020). This effect can be further increased by the presence of non-native species (i.e. dogs and coyotes), whose presence is directly and indirectly favoured by humans. This can have very important consequences for the long-term viability of wildlife populations, for instance, physiological stress caused by a reduction of water intake might affect animal's reproductive success (Crosmary et al. 2012, Tuomainen & Candolin 2011, Wakefield & Attum 2006, Zanette et al. 2011). Additionally, it is known that domestic dogs can harass and prey upon native wildlife, forcing them to avoid usual feeding areas or periods of activity (Hughes & Macdonald 2013, Lenth et al. 2008). Likewise, due to the wide-ranging diet of coyotes, which includes mammals with body sizes ranging from those of mice to deer (Hidalgo-Mihart et al. 2006, Huegel & Rongstad 1985), they can prey upon most of the native mammal and bird species visiting the *sartenejas*. Thus, the presence of these non-native species can increase the occurrence of competitive and predator–prey interactions for the local fauna (Hughes & Macdonald 2013).

A particularly interesting change in animal behaviour, which is very likely a manifestation of the new landscape of fear, is the widespread modification we detected in daily activity patterns in birds and mammals. The species *P. concolor* and *M. pandora* provide the most compelling cases of changes in daily activity patterns by increasing their nocturnality outside the reserve. An increase in

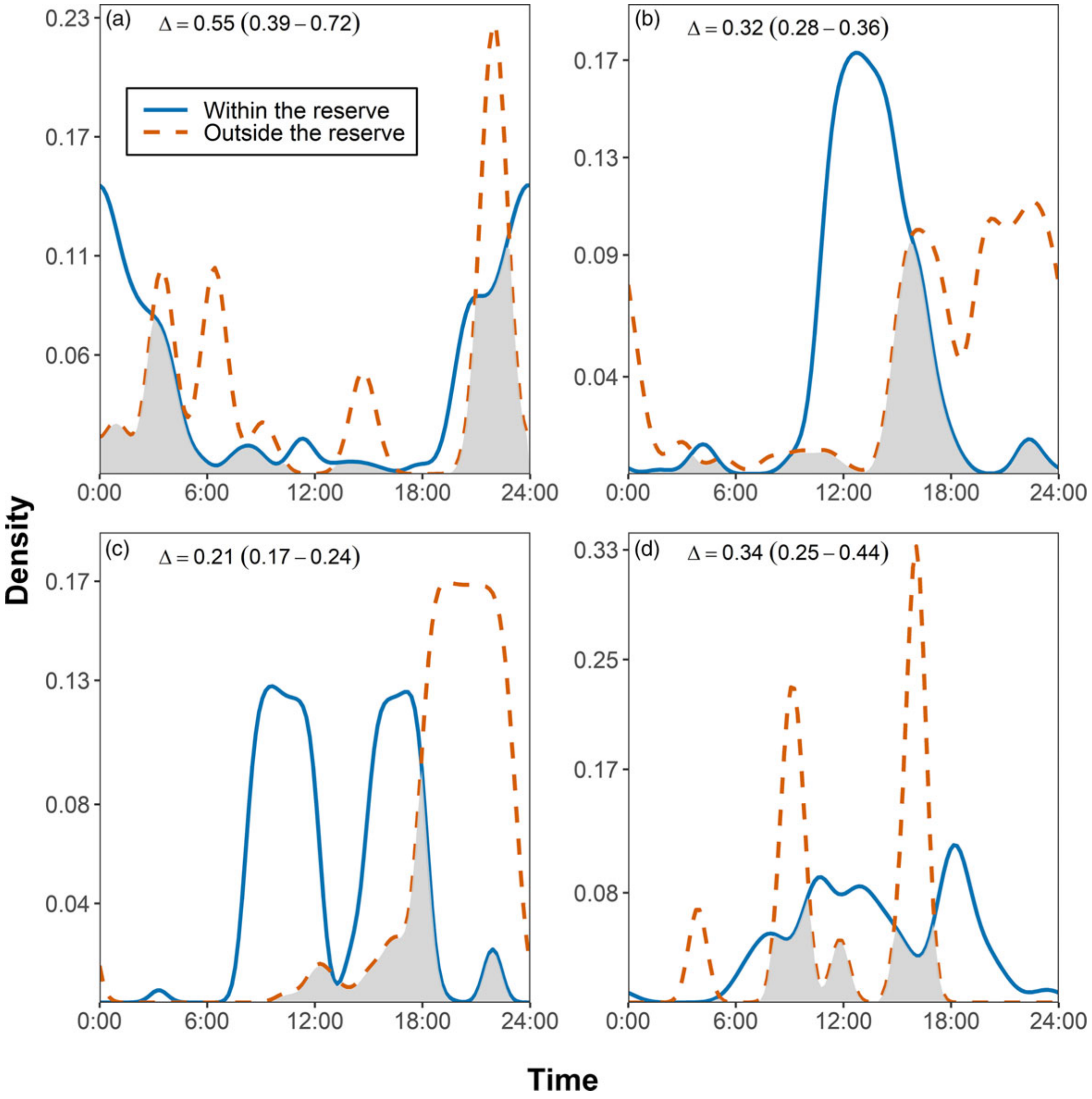

**Figure 3.** Daily activity patterns of mammals using *sartenejas* within and outside the Calakmul Biosphere Reserve (Campeche, southern Mexico): (a) *L. pardalis*, (b) *P. concolor*, (c) *M. pandora*, and (d) *O. virginianus*. The corresponding overlap coefficients (Δ) and 95% confidence intervals are shown in each graph. Gray-shaded areas indicate overlap in activity patterns.

activity during new moon nights was recently reported for *T. bairdii* in a site with hunting pressure in the Calakmul region (Sánchez-Pinzón et al. 2020). Furthermore, recent evidence indicates a widespread increase in nocturnality among medium and large-bodied mammals due to human disturbance (Gaynor et al. 2018). This type of response also has been reported in the case of bird daily activity patterns (Fontúrbel et al. 2021). Therefore, differences in daily activity patterns outside the reserve might be a response to deal with the direct and indirect effects of human activities. Changes in the hours of activity can generate a broad spectrum of negative consequences. For example, temporal shifts in activity patterns 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 (Smith et al. 2018, Suraci et al. 2019, Tuomainen & Candolin 2011).

Not all the species appeared to react negatively to human activities; in fact, some species seemed to be favoured by human activities outside the reserve (i.e. those that were recorded only outside the reserve or increased their frequency of use of *sartenejas*). Most of these species share some life-history traits, such as being omnivorous and having relatively large litters, which likely help them to thrive in human-dominated landscapes (Carrara et al. 2015, Morante-Filho et al. 2015, Samia et al. 2015, Santini et al. 2019, Sol et al. 2014). Interestingly, some of these species showed a negative association with distance to roads (i.e. the shorter the distance the higher the frequency of use) and had increases in the duration of their visits, and only minor changes in daily activity patterns (outside vs. within the reserve). Such responses might be due to the fact these species are not heavily hunted or chased off by local people. It also exists the possibility that these species do not perceive humans as potential predators (Frid & Dill 2002, Sreekar et al. 2015) and that, in some instances, they overlap their activity with that of humans as a way to gain protection against some of their natural predators (Berger 2007, Steyaert et al. 2016).

In summary, our study shows that small-scale frequent human activities have a variety of impacts on wildlife despite forest cover is still extensive. Among these impacts stand out those affecting the composition of bird and mammal assemblages and the behaviour of their species.

### *Conservation implications*

Monitoring of *sartenejas* allowed us to record most of the species in our target groups, including some classified as endangered. Moreover, we obtained the first camera trapping evidence of species such *C. latrans* and *G. vittata* occurring in the communal lands of *Nuevo Conhuas* and the Calakmul Biosphere Reserve, respectively. Therefore, the use of small natural features, providing locally limited resources, such as *sartenejas*, seems to be a promissory approach to detect impacts of human activities on wildlife at the behavioural, population, and community levels.

Much attention has been paid to the impacts large-scale habitat transformations have on tropical wildlife, but much less is known about the impacts of chronic anthropogenic disturbance on tropical vertebrates in regions where extensive forest remains. Our results highlight the urgent need to generate detailed quantitative data to have a more comprehensive understanding of how the different types and magnitudes of human activity impact wildlife.

At the regional scale, the increasing demand for resources in the Calakmul region, combined with the recent increase in drought frequency and disruptions in rainfall patterns caused by global climate change (Mardero et al. 2012, 2020), threatens to decrease, in general, the availability of fresh water for wildlife. Due to the size and hydroperiod of *sartenejas*, these water bodies will, likely, play an increasingly important role as a water source for wildlife inhabiting the region. Therefore, more attention needs to be focused on the monitoring of *sartenejas,* and their inclusion in conservation initiatives conducted in the Calakmul region is highly desirable. During the recent severe droughts that affected the region park guards installed artificial watering points within the reserve to provide water for wildlife. A useful complementary strategy would be to replenish water in *sartenejas* during drought peaks.

**Supplementary material.** To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467421000547

**Acknowledgements.** This contribution is a requirement for C.M.D.M. to obtain his Master's in Biological Sciences (in the field of ecology) of the *Posgrado en Ciencias Biológicas* at Universidad Nacional Autónoma de México (UNAM). We thank the *Posgrado en Ciencias Biológicas* (UNAM). We are very grateful to the people of *Nuevo Conhuas*, especially Doña Mema's family for their hospitality and help during fieldwork as well as to the staff of the regional office of the CONANP. C.M.D.M. was supported by a scholarship from the Mexican National Council of Science and Technology (CONACyT, 629544). E.M. and M.K. were supported by the Sistema Nacional de Investigadores (SNI, National System of Researchers) while conducting this research. We thank G. Gutiérrez-Granados for providing very useful comments on an early draft of this manuscript.

**Financial support.** This work was supported by the Rufford Foundation (C.M.D.M., grant number 24083-1); the National Geographic Society (C.M.D.M., grant number EC-196R-18); and Idea Wild with an equipment grant to C.M.D.M.

**Conflict of interest.** None.

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