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Terrestrial mammals' species richness: diversity and activity patterns in the Darién National Park, Panamá

Riqueza de mamíferos terrestres: diversidad y patrones de actividad en el Parque Nacional Darién, Panamá

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Darién National Park is one of the largest forest blocks of Mesoamerica. Monitoring terrestrial mammal species in this region is essential to define adequate conservation actions to ensure their long-term persistence. We deployed 33 camera trap stations at the Darién National Park and evaluated the relative abundance of terrestrial mammal species, the sampling effort needed to estimate reliable richness estimates, and the activity patterns of the most recorded species. We identified with certainty 24 species of terrestrial mammals. Our survey was quite representative since we detected 85 % of the species that had previously been recorded for this area. Jaguars (*Panthera onca*), ocelots (*Leopardus pardalis*), and margays (*L. wiedii*) showed crepuscular behavior, and pumas (*Puma concolor*) and jaguarundis (*P. yagouaroundi*) showed diurnal behavior. Species that showed more activity during periods of more light were the ñeque (*Dasyprocta puntancta*), coati (*Nasua narica*), temazate (*Mazama temama*), and both species peccaries (*Tayassu pecari* and *Pecari tajacu*). Species with more nocturnal activity were the paca (*Cuniculus paca*), nine-banded armadillo (*Dasypus novemcinctus*), and Baird's tapir (*Tapirus bairdii*). This one of the first studies that evaluates the activity patterns of terrestrial mammals in the Darién and Panamá. We recorded some species that have not been documented in previous camera trapping studies for the region. However, the richness estimators indicated that there are still species that could be detected. Implementation of long-term monitoring programs is a crucial step to better understanding the dynamics of wildlife populations in the region.

Key words: Animal inventory; camera trapping; Panamá isthmus; species accumulation curves; tropical rain forest; wildlife monitoring.

El Parque Nacional Darién, es uno de los mayores bosques de Mesoamérica y el monitoreo de las poblaciones de mamíferos terrestres en esta región es fundamental para definir acciones de conservación que aseguren su persistencia. Colocamos 33 estaciones de foto trampeo y evaluamos la abundancia relativa de los mamíferos terrestres, el esfuerzo de muestreo necesario para obtener una estimación confiable de su riqueza y los patrones de actividad de las especies más registradas. Identificamos con certeza 24 especies de mamíferos. Nuestro muestreo fue representativo, ya que documentamos el 85 % de las especies que ya se habían registrado para esta área. Los jaguares (*Panthera onca*), ocelotes (*Leopardus pardalis*) y margays (*L. wiedii*) mostraron un comportamiento crepuscular, y los pumas (*Puma concolor*) y jaguarundis (*P. yagouaroundi*) un comportamiento diurno. El ñeque (*Dasyprocta puntancta*), el coatí (*Nasua narica*), el temazate (*Mazama temama*) y ambas especies de pecaríes (*Tayassu pecari* y *Pecari tajacu*) mostraron mayor actividad diurna. La paca (*Cuniculus paca*), el armadillo de nueve bandas (*Dasypus novemcinctus*) y el tapir (*Tapirus bairdii*) mostraron mayor actividad nocturna. Este es uno de los primeros estudios que evalúa los patrones de actividad de los mamíferos terrestres para el Darién y todo Panamá. Documentamos algunas especies que no habían sido registradas en estudios previos para la región. Sin embargo, los estimadores de riqueza indicaron que aún existen más especies que podrían ser detectadas. La implementación de programas de monitoreo a largo plazo es un paso crucial para comprender mejor la dinámica de las poblaciones de vida silvestre en la región.

Palabras clave: Bosque lluvioso tropical; curvas de acumulación de especies; foto-trampeo; inventario animal; Istmo de Panamá; monitoreo de vida silvestre.

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Panamá, together with the entire Central American region, is one of the countries with the greatest biodiversity in the world, housing between 5 to 12 % of the species present on the planet in just 0.5 % of the earth's surface (Mittermeier *et al.* 1997; Myers *et al.* 2000; Meyer *et al.* 2020). Panamá is located in the southernmost of the Mesoamerican region, where the forests of the Darién province expand to one of the largest tropical rainforest masses in the American Continent: the Colombian Chocó (Moreno *et al.* 2016). This region, including the Darién National Park, is precisely one of the largest tropical rainforest blocks in Panamá where 174 mammal species have been recorded and is one of the places in the region where species such as the jaguar (*Panthera onca*), Baird' tapir (*Tapirus bairdii*) and

white-lipped peccary (*Tayassu pecari*) could persist long-term (Sanderson *et al.* 2002; ANAM 2007; Moreno *et al.* 2016; de la Torre *et al.* 2018a; Schank *et al.* 2020; Thornton *et al.* 2020). For this reason, monitoring these and other mammal species populations within the Darién National Park is essential to understand their conservation status in the region, and to define adequate management and conservation actions to ensure their long-term persistence.

Monitoring of terrestrial mammal species implies a great challenge, since most of these species are cryptic, secretive, and nocturnal, which makes it difficult to observe them directly in the field (Trolle 2003; Yasuda 2004; Rovero and Marshall 2009). However, the monitoring of terrestrial mammals' populations through camera trapping has become a very widespread tool in the last decade, and this technique has been used to estimate densities of species such as the jaguar, ocelot (*Leopardus pardalis*), puma (*Puma concolor*), Bairds' tapir in Mesoamerica (Silver *et al.* 2004; Dillon and Kelly 2007; Kelly *et al.* 2008; de la Torre and Medellín 2011; de la Torre *et al.* 2016; Harmsen *et al.* 2017; Rivero *et al.* 2021). Furthermore, the information obtained through the camera traps also allows to study of other aspects of terrestrial mammals, such as their activity patterns or circadian cycles (Monroy-Vilchis *et al.* 2009; Romero-Muñoz *et al.* 2010; Foster *et al.* 2013; Briones-Salas *et al.* 2016), the habitat features that are associated positively and negatively with their occurrence (Monroy-Vilchis *et al.* 2009; Foster *et al.* 2010; de la Torre *et al.* 2018b), as well as the interactions between the different species (Harmsen *et al.* 2009; Monroy-Vilchis *et al.* 2009; Foster *et al.* 2010, 2013). For this reason, Fundación Yaguará Panamá since 2014 has focused on monitoring the jaguar and other emblematic species, such as the Bairds' tapir and the white-lipped peccary, in the Darién National Park through camera traps to generate a robust baseline that can help guide future conservation actions focused on these species throughout this region. Evaluating the diversity and abundance of terrestrial mammals in the long term will allow us to understand if the protection scheme in this region is helping to maintain the populations of emblematic species, as well as document the presence of rare or threatened species to improve their conservation in the region. In addition, understanding the activity patterns of these species will allow establishing a baseline to assess the impact that human activities and other disturbances could have on the behavior of these species, in order to improve the management of the protected areas in the region.

In this study, we examined the terrestrial mammals' species richness and activity patterns in the Darién National Park, Panamá. We used the camera trapping technique to test the hypothesis that the terrestrial mammal community in the Darién National Park has high species richness and a high occurrence of large mammal species. We also evaluated the activity patterns of the most recorded species, and we classified their activity as diurnal, nocturnal, cathemeral, or crepuscular to test the hypothesis that their activity patterns are similar to those reported to other regions of their distribution range.

Study area. Our study area was in the Serranía de Pirre within the Darién National Park, Panamá (Figure 1a). Darién National Park is located at the southernmost end of the land bridge between Central and South America (Claudino-Sales 2019). This region is one of the most species-rich expanses of lowland and highland rainforests in the world and contains a great occurrence of endemism over a broad range of taxa (Walshburger *et al.* 2008; Méndez-Carvajal *et al.* 2021). Annual rainfall ranges between 3,000 mm-4,000 mm and there is a marked dry season with less than 100 mm a month from January through March. The mean temperature ranges between 16 °C-35 °C, with an annual mean of 26 °C (Claudino-Sales 2019). Tropical rainforests of Darién National Park are relatively undisturbed and contain the most diverse and species-rich terrestrial ecosystems of tropical Central America (Walshburger *et al.* 2008; Meyer *et al.* 2015a; Claudino-Sales 2019; Méndez-Carvajal *et al.* 2021).

Survey design. Our study was accomplished using the camera trapping technique. We deployed the camera traps using the pre-existed trails that occur in the Serranía de Pirre inside the Darién National Park, and the survey was carried out from October 2020 to May 2021. We placed 33 camera trap stations which were active at different times during the sampling period giving a final sampling effort of 3,465 camera trap days. Due to the limited number of camera traps available for the study and the high incidence of equipment theft in the region, we decided to implement this survey using different blocks to cover as much surface as possible of the National Park and surrounding forest areas. Some camera trap stations were active from October 2020 to the end of March 2021, while others were only active from October 2020 to December 2020, or from March to May 2021, December 2020 to May 2021, and other camera trap stations were stolen (Figure 1b; Table 1). For this reason, the sampling effort was considered continuous using different temporal sampling blocks (Figure 1b; Table 1), although not all the stations were active during the entire period of the 219 days that the survey lasted.

Camera trap stations were placed 1-3 km apart and in sites where terrestrial mammals' signs were previously observed. To increase the probability of detection, all camera trap stations were set out with 2 camera traps, one on either side of the trail, to photograph simultaneously both sides of the animals that passed along the trails. In each camera trap station, 1 of the cameras was configured to take a video 15 sec long for each detection, and the other one was configured to take 3 pictures for each detection. Camera traps were positioned 40-50 cm above the ground, and at least 3 m off the trail where we expected the animals to pass.

Data analysis. To have an estimate of the species richness of large and medium mammals in our study area, we identified the species in the photographs and videos obtained through camera traps (Reid 2009). We identified all the species of mammals recorded at the species level

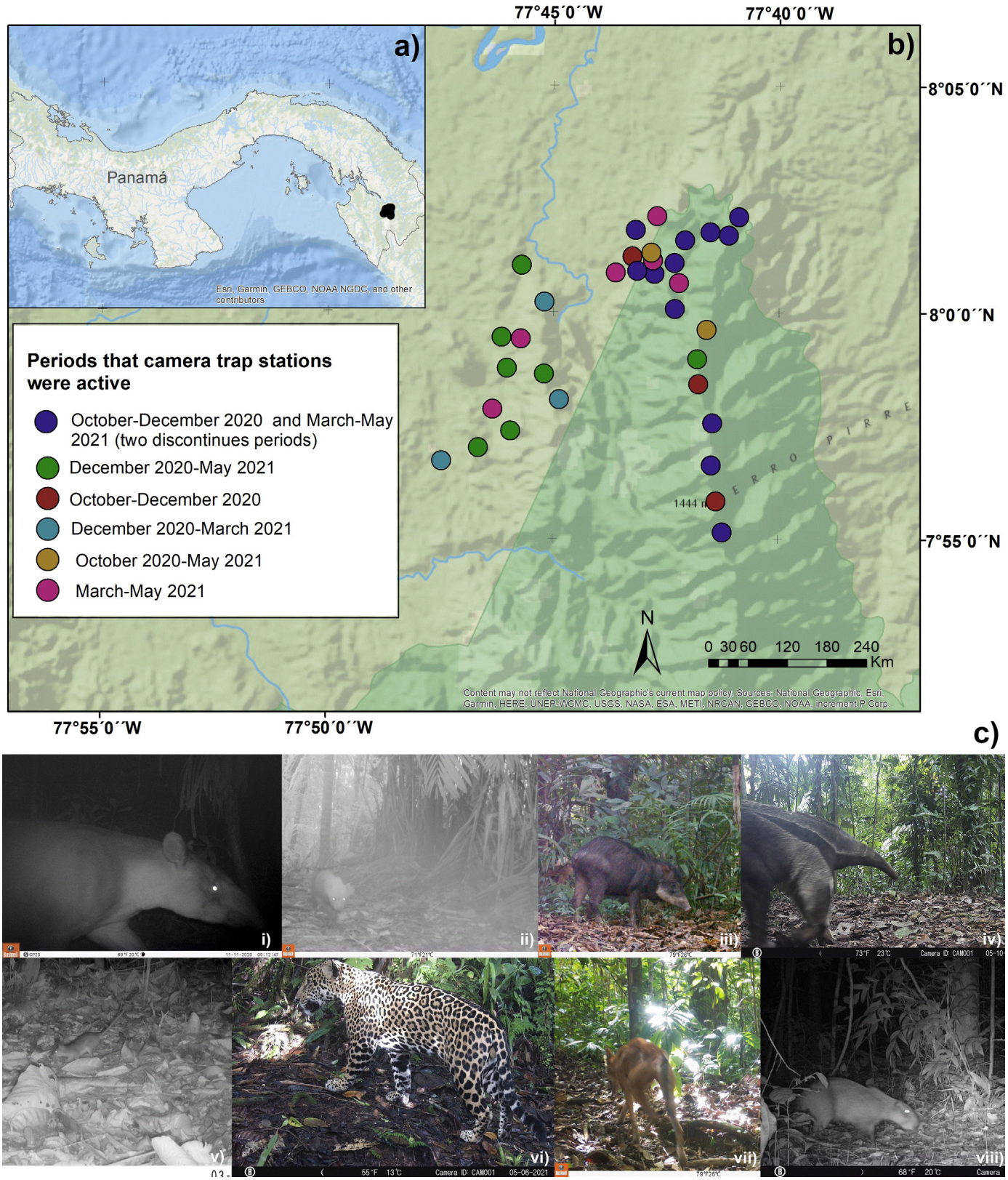

Figure 1. a) Localization of our study area in Panamá. b) Spatial and temporal distribution of the camera trap stations used in this study in the Darién National Park, Panamá. c) Images obtained by the camera traps of the terrestrial mammals of the Darién National Park, Panamá: i) *Tapirus bairdii*; ii) *Speothos venaticus*; iii) *Tayassu pecari*; iv) *Myrmecophaga tridactyla*; v) *Marmosa* sp.; vi) *Panthera onca*; vii) *Canis latrans*; vii) *Hydrochoerus isthmius*.

whenever it was possible. Species identified included large ones (> 10 kg) such as the Bairds' tapir (250 kg), to medium ones (101 g-10 kg) such as the tropical rabbit (*Sylvilagus brasiliensis*–1 kg), and small ones (1-100 g) such as the red tail squirrel (*Sciurus granatensis*–350 g). However, most of the recorded species are considered medium or large mammal species (Ceballos and Oliva 2005; Reid 2009). To obtain a proxy of the abundance of the medium and large

terrestrial mammal species in the Darién National Park, we evaluated the relative abundance of these species by calculating the number of independent records per each 1,000 camera trap days through the following formula (Chávez *et al.* 2014):

(Number of independent records * 1,000) / the total effort calculated in trap days.

Independent records were calculated using the independence criteria for each record of an hourly interval, that is, if a record of a species was obtained at a camera trap station it was considered a new independent record until 60 min had elapsed from the first record (Chávez *et al.* 2014). Group species were considered as only 1 record without considering the number of individuals recorded by the camera traps.

To evaluate if our survey was well represented, we used species-accumulation curves graphing the addition of new species as the sampling effort on camera trap days increased along the sampling. We also evaluated the performance of 6 incidence-based nonparametric richness estimators: ICE, Chao 2, Jackknife 1, Jackknife 2, Bootstrap, and MMRuns (Colwell and Coddington 1994; Colwell 2006). Because nonparametric species richness estimators are directly related to the closed population of capture-recapture models, one of the assumptions is that the species community composition did not change over the survey time, which means that the community was closed to the colonization of new species or migration (Tobler *et al.* 2008). So then, we assumed that the continuous duration of 219 days of our survey did not violate this assumption.

We used EstimateS to compute the rarefaction curves and nonparametric richness estimators, and we used 1,000 randomizations for the analysis (Colwell 2006). For all richness estimators, we plotted the resulting curves using the sampling effort in camera trap days on the X-axis. To assess the integrity of our sampling and the precision of the total number of species estimated by the different estimators, we compared the resulting number of species with a list of terrestrial mammal species also obtained by camera trapping for the study area (Meyer *et al.* 2015a).

In order to understand the activity patterns of the terrestrial mammals that occur in Darién National Park, we registered the time of each record of these species during the survey. Analysis of this information was done through the "activity" package for R (Rowcliffe 2015). For this analysis, we only used the independent records obtained at time intervals of 1 hr between each one. To estimate the activity patterns, the times recorded were converted into their 24-hr equivalence in a ratio of 0 to 1. These analyses were only implemented with those species that had more than 15 independent records during the survey, and we classified the activity preference of the most recorded species as diurnal (< 20 % of observation in the dark period), nocturnal (> 80 % of observations in the dark period), crepuscular (> 50 % of observations during the crepuscular phase), or cathemeral activity (sporadic and random intervals of activity during the light and dark periods (Jiménez *et al.* 2010; Gray and Phan 2011; Botts *et al.* 2020).

During the survey, we clearly identified a total of 24 species of terrestrial mammals in the 33 camera trap stations (potentially 25 since we registered a marsupial of the *Marmosa* genus that likely is *Marmosa isthmica*; Figure 1c; Table 2). The 4 species with the highest relative abundance were the ñeque (*Dasyprocta punctacta*), followed by the collared peccary (*Pecari tajacu*), the red-tailed squirrel (*Sciurus granatensis*), and the ocelot (*L. pardalis*). The 4 species with the lowest number of records were the bush dog (*Speothos venaticus*), the coyote (*Canis latrans*), the lesser capybara (*Hydrochoerus isthmius*), and the tropical rabbit (*Sylvilagus brasiliensis*; Table 1).

Results showed that our survey was quite representative since we recorded 85 % of the terrestrial mammal species that had previously been recorded for this area using the camera trapping technique (Meyer *et al.* 2015a). Even during the camera trap survey, rare and difficult-to-record species in the region such as the bush dog (*S. venaticus*), coyote (*C. latrans*), and giant anteater (*Myrmecophaga tridactyla*) were recorded. However, the results of the richness estimators evaluated, except for the MMRuns, indicated a negative bias in our sampling and that some rare and secretive species were still missing from our survey (Figure 2a).

The results of activity patterns analyses showed that jaguars, ocelots, and margays (*L. wiedii*) have crepuscular behavior, having their activity peaks during sunrise and sunset (Figure 2b). Pumas and jaguarundis (*Puma yagouaroundi*) showed more diurnal behavior, showing more activity during the hours with more light throughout the

Table 1. Camera trapping sampling blocks used in the Darién National Park, Panamá including the sampling periods of each of the blocks and the number of camera traps stations used in each block.

Block ID	Sampling periods	Camera trap stations in this block
1	October-December 2020 and March-May 2021 (2 discontinues periods)	12
2	December 2020-May 2021	7
3	October-December 2020	3
4	December 2020-March 2021	3
5	October 2020-May 2021	2
6	March-May 2021	6

day (Figure 2b). The species that showed more activity during periods of more light during the day were the ñeque, coati (*Nasua narica*), venado corzo (*Mazama temama*), and both species peccaries (*T. pecari* and *Pecari tajacu*; Figure 2b). In contrast, the species with the most activity at night were the paca (*Cuniculus paca*), the nine-banded armadillo (*Dasypus novemcinctus*), and Baird's tapir (Figure 2b).

Results of species accumulation curves showed that our survey was quite representative since practically 85 % of the species that had previously been recorded using the camera trapping technique for this area were recorded in this survey (Meyer *et al.* 2015a). Our results supported our prediction that the terrestrial mammal community in the Darién National Park has high species richness and a high

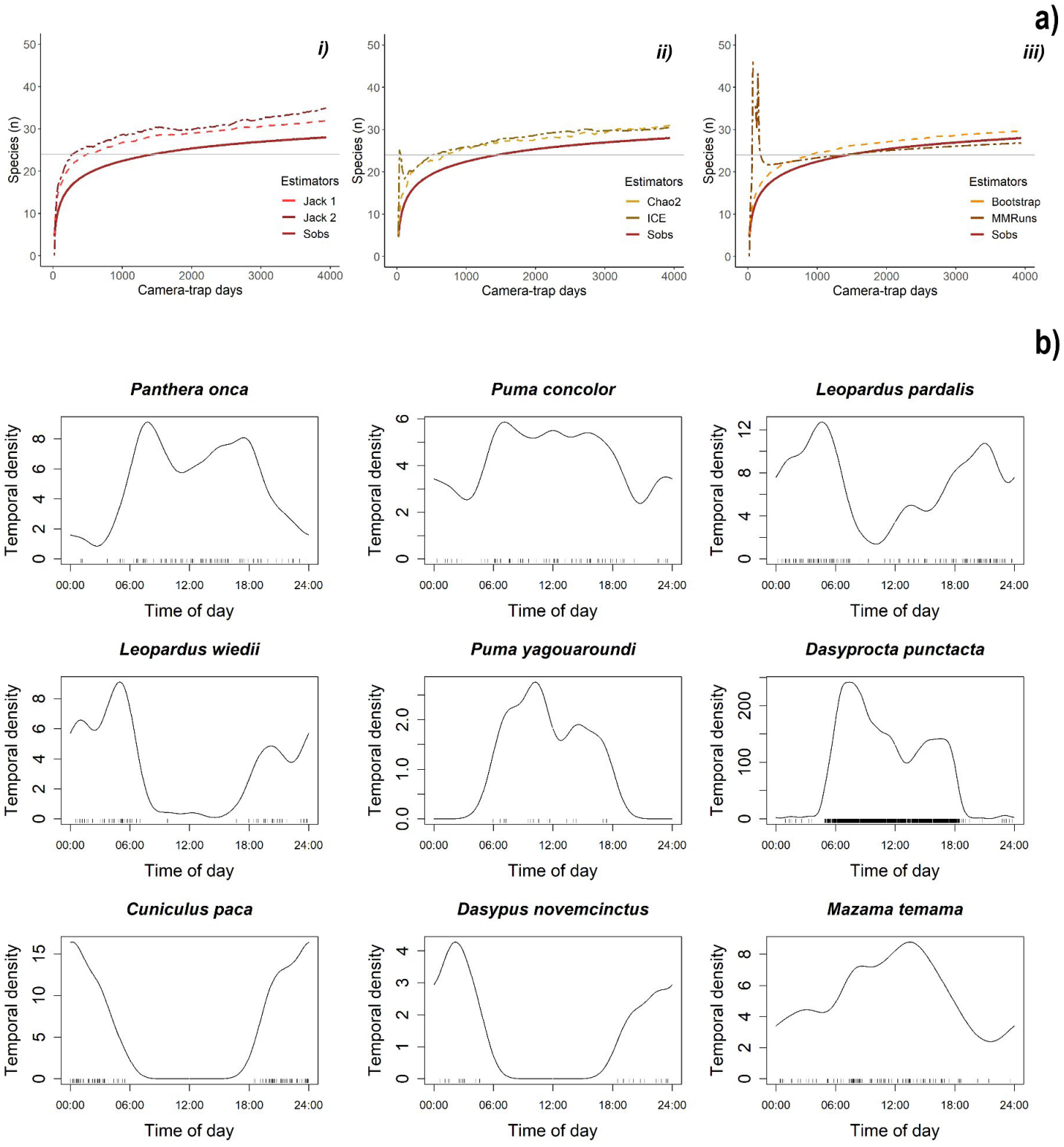

Figure 2. a) Comparison of the different richness estimators for medium and large terrestrial mammals' species for the data obtained in the survey in the National Park Darién, Panamá: i) Jackknife 1 and Jackknife 2; ii) ICE and Chao 2; and iii) Bootstrap and MMRuns. The number of species previously recorded for the region in other studies with camera traps was 26 (Meyer *et al.* 2015a). b) Activity patterns of the most recorded medium and large terrestrial mammal species in the Darién National Park, Panamá.

occurrence of large mammal species, such as the jaguar, white-lipped peccary, and Baird's tapir. Furthermore, we recorded other species that have not been documented in other studies that have used the camera trapping technique in the region, such as the lesser capybara, coyote, and potentially Robinson's mouse opossum (*M. robinsoni*; Table 2). Also, the results showed that monitoring using camera trapping technique is quite useful to register species that could be considered rare, since during our survey we recorded species such as the bush dog (*S. venaticus*), which is difficult to detect but it is potentially expanding its range towards the Panama Bridge (Meyer *et al.* 2015b).

Similarly, to other studies implemented with camera traps in the region (Meyer *et al.* 2015a), our results demonstrated the camera trapping technique's efficiency in assessing the species richness and relative abundance of the terrestrial mammal species that occur within the Darién National Park. However, the richness non-parametric estimators predicted that there are still species to be detected, this is probably because some species with a very low probability of detection were not recorded in our survey, such as species with more arboreal or aquatic habits than terrestrial, or by their secretive nature. This could happen with species such as the weasel (*Mustela frenata*), the greater grison (*Galictis vitatta*), the river otter (*Lontra longicaudis*), Allen's olingo (*Bassaricyon alleni*), kinkajou (*Potos flavus*) and porcupine (*Coendou rosthchildi*). Since that in our survey, we probably detected most of the species in the study area (more than 75 % of the species present in the region) and since the probability of detection is highly variable among the recorded species, the more likely richness estimator for our survey could be the Jack 1 and Jack 2 (Tobler

Table 2. Species recorded during the survey in Darién National Park, Panamá including the total number of records, independent records, and relative abundance of these species.

Class	Order / Family	Species	Total records obtained	Independent records (1 hour)	Relative abundance	Activity pattern
MAMMALIA	DIDELPHIMORPHIA					
	Didelphidae	*Didelphis marsupialis*	264	93	26.84	Nocturnal
		Marmosa sp. (likely *M. isthmica*)	4	4	1.15	-
		Unidentified opossums (*Metachirus nudicaudatus* or *Philander opossum*)	68	29	8.37	-
	CINGULATA					
	Dasypodidae	*Dasypus novemcintus*	232	33	9.52	Nocturnal
	PILOSA					
	Myrmecophagidae	*Tamandua mexicana*	42	9	2.60	Cathemeral
		Myrmecophaga tridactyla	32	6	1.73	Diurnal
	RODENTIA					
	Caviidae	*Hydrochoerus isthmius*	12	1	0.29	-
	Cuniculidae	*Cuniculus paca*	499	133	38.38	Nocturnal
	Dasyproctidae	*Dasyprocta puntacta*	15,648	2,125	613.28	Diurnal
	Echimyidae	Unidentified rodent	99	44	12.70	-
	Sciuridae	*Sciurus granatensis*	730	221	63.78	Diurnal
	LAGOMORPHA					
	Leporidae	*Sylvilagus brasiliensis*	2	2	0.58	-
	CARNIVORA					
	Canidae	*Cerdocyon thous*	9	3	0.87	-
		Canis latrans	1	1	0.29	-
		Speothos venaticus	2	1	0.29	-
	Felidae	*Leopardus wiedii*	224	82	23.67	Crepuscular
		Leopardus pardalis	658	170	49.06	Crepuscular
		Puma yagouaroundi	101	26	7.50	Diurnal
		Puma concolor	469	103	29.73	Cathemeral
		Panthera onca	702	123	35.50	Crepuscular
	Mustelidae	*Eira barbara*	119	21	6.06	Diurnal
	Procyonidae	*Nasua narica*	136	24	6.93	Diurnal
		Procyon cancrivorus	14	7	2.02	-
	PERISSODACTYLA					
	Tapiridae	*Tapirus bairdii*	97	15	4.33	Nocturnal
	ARTIODACTYLA					
	Cervidae	*Mazama temama*	993	132	38.10	Diurnal
	Tayassuidae	*Tayassu pecari*	289	18	5.19	Diurnal
		Pecari tajacu	7,361	257	74.17	Diurnal

et al. 2008). This would indicate that species richness that could be detected using the camera trapping technique in our study area would range between 28 and 32 species.

Results supported our hypothesis that activity patterns of the most recorded species are similar in Darién National Park to those reported in other regions of their distribution range. Activity patterns analyses showed that the top predator of this ecosystem, the jaguar, has a crepuscular behavior, with its activity peaks during sunrise and sunset, which is similar to what has been found in other tropical forests, but also in dry, and temperate forests of México and South America (Monroy-Vilchis *et al.* 2009; Di Bitetti *et al.* 2010; Romero-Muñoz *et al.* 2010; Hernández-Saintmartín *et al.* 2013; Briones-Salas *et al.* 2016). Otherwise, ocelots and margays were also crepuscular, but their activity decreased significantly during the brightest hours of the day, and pumas and jaguarundis showed more diurnal behavior, displaying more activity during the brightest hours of the day. These differences between the felid species in their activity patterns could be a mechanism that allows their coexistence in areas of sympatry (Di Bitetti *et al.* 2010). Jaguars and pumas showed a high overlap, although pumas were more active during the daylight hours. In the case of small felids, the temporal segregation pattern is clearer, jaguarundis have more diurnal habits compared to ocelots and margays, and potentially segregation between ocelots and margays occurs in spatial terms since margays have more arboreal habits (Di Bitetti *et al.* 2010).

Regarding other species, the ones that showed more activity during the periods of more light during the day were the ñeque, the coati, the venado corzo, and both species of peccaries (Figure 2b). These species have shown similar diurnal activity patterns in other regions of Mesoamerica such as Costa Rica, and southern México (Pérez-Irineo and Santos-Moreno 2016; Arroyo-Arce *et al.* 2017; Botts *et al.* 2020; Falconi-Briones *et al.* 2022). However, venado corzo has shown cathemeral activity patterns in the tropical rainforests of Oaxaca, México (Pérez-Irineo and Santos-Moreno 2016). In contrast, the species with more activity during the night were the nine-banded armadillo, the paca, and Baird's tapir (Figure 2b). Nine-banded armadillos have been classified as nocturnal species by several studies, though they can change their activity patterns according to environmental conditions, such as forest patch sizes (Norris *et al.* 2010). Pacas have shown nocturnal activity patterns in the tropical forests of Costa Rica and the Humid Chaco in Argentina (Arroyo-Arce *et al.* 2017; Huck *et al.* 2017; Botts *et al.* 2020). In general Baird´s tapirs show nocturnal activities in the tropical rainforest of southern México, and in most of their distribution ranges (Pérez-Irineo and Santos-Moreno 2016; Falconi-Briones *et al.* 2022; Sánchez-Pinzón *et al.* 2020), but in some areas such as montane forests in México shown cathemeral activity (Carbajal-Borges *et al.* 2014).

This study demonstrates the efficiency of the camera trapping technique to be implemented in the biological monitoring of the region to evaluate year after year the state of conservation of the Darién National Park. Implementation of long-term monitoring programs is a crucial step to better understanding the dynamics of wildlife populations within the National Park because these will add information to evaluate different aspects of the basic ecology of emblematic species. It is necessary to replicate these kinds of efforts in other large forest blocks in Mesoamerica to monitor the occurrence and conservation status of wildlife in these wild areas.

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