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Birds on camera: assessing avifaunal detections by camera traps in the Amazon

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Master of Science in Tropical Ecology and Management of Natural Resources

Acknowledgements

Since starting at the Norwegian University of Life Sciences six years ago, the dream has been a master thesis on tropical birds with fieldwork in Amazonia. Alas, COVID-19 crushed fieldwork plans; research on beach nesting avifauna along the Juruá river in Brazil had to be discarded. Stuck in Ås, I probably got the second-best option to being in the Amazon – processing thousands of camera trap images from this diverse rainforest.

Without the camera trap images provided by Elildo Carvalho Jr. and Torbjørn Haugaasen, this thesis in tropical ecology would not have been possible. The camera trap data was collected as part of the National Biodiversity Monitoring Program of *Instituto Chico Mendes de Conservação da Biodiversidade* (*Programa Monitora* ICMBio – Brazilian Ministry of the Environment) and the work was funded by *Programa Áreas Protegidas da Amazônia* (ARPA). Therefore, I want to recognise the ICMBio staff and volunteers who installed and picked up camera traps and viewed the images the first-time round.

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Abstract

Camera traps have become an increasingly useful tool for biodiversity surveys in tropical forests, but most of these studies focus on larger-bodied terrestrial vertebrates, particularly mammals. To date few camera trap surveys specifically target birds, yet studies on vertebrates represent a potentially valuable data source if incidentally recorded avifauna can be reliably identified from existing camera trap images. This thesis is one of the first studies to attempt identification of all avian species captured via camera traps, using ground-based arrays at three sites in the Brazilian Amazon. Data were used to analyse species richness, the functional traits of the detected avian species, and the activity patterns observed across the detected bird taxa. Sampling occurred in three protected areas: Terra do Meio Ecological Station, Juruena National Park, and Jamari National Forest. Camera trap surveys followed the Tropical Ecology Assessment and Monitoring (TEAM) network protocol for monitoring terrestrial vertebrates in tropical forests as part of the National Biodiversity Monitoring Program of *Instituto Chico Mendes de Conservação da Biodiversidade* (*Programa Monitora* ICMBio – Brazilian Ministry of the Environment). In total, 53,546 images with birds were captured, in which 66 species were identified, including the notable detections of two little-known species *Nothocrax urumutum* and *Neomorphus squamiger*. Terrestrial avifauna were detected at a rate three times higher than species from higher forest strata, with the highest detection rates found in larger, ground-dwelling species. The observed activity patterns indicate a behavioural response to heat stress. Generally, terrestrial avifauna were most active in the cooler mornings and evenings, but certain families showed a less prominent bimodal diurnal activity. On the other hand, arboreal species were mostly detected towards noon, probably escaping to the shadier understorey during the hottest hours. Although this study demonstrates the high value of camera traps in surveying cryptic or elusive terrestrial avifauna, it also shows that smaller species are less likely to be detected, and higher forest strata species are only observed when these might come down to the forest floor.

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The Amazonian rainforest is one of the most biodiverse areas on the planet. Harbouring around 1,300 bird species, the Amazonian avifauna is exceptionally rich (BirdLife International, n.d.; Haffer, 1969; Terborgh et al., 1990; Terborgh et al., 1984). High mean annual temperature and rainfall increase primary productivity providing an abundance of resources to support more species and a diversity of guilds (Brown, 2014; Hanya & Aiba, 2010; Marra & Remsen Jr, 1997). In addition, the diversity of microhabitats characterising the Amazon promote niche specialisation within species, where most of these species are rare (Hill & Hill, 2001; MacArthur & MacArthur, 1961). Due to this immense diversity and rarity, obtaining a representative inventory of the avian species present at a site is time consuming and strenuous (Bibby et al., 2000; Stevens et al., 2019; Terborgh et al., 1990). Knowledge on avian communities and the species' distributions in Amazonia is therefore not as comprehensive as in temperate regions (Terborgh et al., 1990).

Several survey methods for bird inventories exist, each with their own strengths and weaknesses. The most traditional methods are line-transecting, point counts, audio-records, and capture techniques such as mist-netting (Bibby et al., 2000). These are effective sampling techniques, but are labour intensive and largely restricted to more accessible areas (Silveira et al., 2003; Stevens et al., 2019; Trolliet et al., 2014) during daylight hours – thus excluding nocturnal species (Moore et al., 2020). In species rich regions like the Amazon, field workers must also be extremely skilled in rapid identification of both appearance and vocalisations of a large number of species (Bibby et al., 2000; Silveira et al., 2003; Terborgh et al., 1990). Furthermore, human presence may alter behaviour (Bridges & Noss, 2011; O'Brien & Kinnaird, 2008; Silveira et al., 2003; Suwanrat et al., 2015). These weaknesses indicate a need for less invasive sampling methods (Stevens et al., 2019).

Motion- and heat-triggered wildlife cameras, hereafter referred to as camera traps, are remotely triggered camera systems (Swann et al., 2011). This technology has developed significantly over recent years and is now commonplace in ecological research (Kucera & Barrett, 2011; Trolliet et al., 2014). Camera traps have been mostly used in mammal research, but their use in avian studies is also increasing, for example in investigating species richness, the presence of rare or elusive species, and temporal behaviour (Burton et al., 2015; Kucera & Barrett, 2011; O'Brien & Kinnaird, 2008; Swann et al., 2011; Trolliet et al., 2014). Camera traps operate throughout the diel cycle, are non-invasive, can be left in the field for several weeks, can be installed in more remote places, and require minimal human labour for instalment (Beaudrot et al., 2016; Kays et al., 2010; Lashley et al., 2018; O'Brien & Kinnaird, 2008). The non-invasive and cost-efficient nature of these cameras has made them one of the most used tools in monitoring behaviour and population dynamics in the wild (Rovero & Ahumada, 2017).

However, despite the several benefits of camera traps, cameras are normally placed at knee hight, creating a major disadvantage for avian studies. Tropical rainforests have characteristically high trees, where each stratum has distinguishable environmental conditions (Bibby et al., 2000; Walther, 2002a). In the Amazon and other tropical forests, avian diversity is highest in the canopy (Chmel et al., 2016; Pearson, 1971; Terborgh et al., 1984). Several avian species have adapted to foraging in specific forest strata and the conditions within, restricting movement to their niche (Marra & Remsen Jr, 1997; Walther, 2002a). Therefore, detecting species residing in arboreal strata is less likely and ground-based camera trap data are thus biased towards ground-dwelling and understorey species (Chmel et al., 2016). In addition, the most frequently used camera trap set-ups are more suitable for sampling larger birds, hence detections are more likely skewed towards large species (Kays et al., 2010; O'Brien & Kinnaird, 2008).

For such species, camera traps can be used to obtain activity pattern data. Contrary to telemetry tracking, handling of animals is not required and behaviour is not obscured by human presence (Bridges & Noss, 2011; Carthew & Slater, 1991; Frey et al., 2017). Time-stamped images raise the opportunity for activity pattern analyses throughout the diel cycle and give insight on temporal responses to stress factors such as heat and competition (Frey et al., 2017; Rowcliffe et al., 2014; Sollmann, 2018; Trolliet et al., 2014). Moreover, activity data on several species are obtained through the same cameras (Bridges & Noss, 2011; Rovero et al., 2010), increasing our knowledge of how species and populations behave on a temporal scale in their natural environment.

Occasional records of particularly cryptic and shy terrestrial and understorey birds may also be obtained, increasing the natural history knowledge of such species. Cryptic and shy species are difficult to detect but with camera traps in the field for several months, the chances of observing these birds increase (Bridges & Noss, 2011; O'Brien & Kinnaird, 2008; O'Connell et al., 2011). For example, a better understanding on the spatial and temporal behaviour of the secretive and rare *Tinamus solitarius* was obtained through camera trap surveys (Kuhnen et al., 2013). In Sumatra, new distribution data was obtained on the little-known Sumatran Ground Cuckoo (*Carpococcyx viridis*) through camera trap images, and seven endemic ground-dwelling avian species were unknown to science until detected on camera trap footage by chance (Dinata et al., 2008; O'Brien & Kinnaird, 2008).

In the Amazon, few camera trap studies focus solely on birds and certain detections are normally excluded. For example, studies targeting both ground-dwelling mammals and birds, usually exclude data on smaller species (Blake et al., 2017; Carvalho Jr et al., 2020; Costa et al., 2018; Negroes et al., 2011) – even if they focus on particular landscape features, such as mineral licks (Blake et al., 2011; Griffiths et al., 2020). Studies that focus only on the avifauna, such as Mere Roncal et al. (2019) only include the larger ground-dwelling species and ignore smaller birds like the passerines. Yet, species outside the targeted strata and size are

occasionally detected and allow for interesting data to be analysed (Burton et al., 2015; Murphy et al., 2018).

To my knowledge, this is the first study for the Amazon region to include all avian species captured on camera traps. Camera traps collect large amounts of data, but when certain detections are automatically excluded, the potential knowledge we could obtain on several species is ignored (Dinata et al., 2008; Lamelas-Lopez et al., 2020; Murphy et al., 2018; O'Brien & Kinnaird, 2008). Therefore, in this study, I use a large camera trap dataset from three protected areas in the Brazilian Amazon and attempt to identify all avian species captured. More specifically, I investigated: 1) Which avian species were detected by camera traps and what traits characterise these bird species? 2) What activity patterns were observed across bird taxa and did these differ between sites and foraging strata? The results are discussed in relation to previous studies in the region and the known natural history of particular bird taxa.

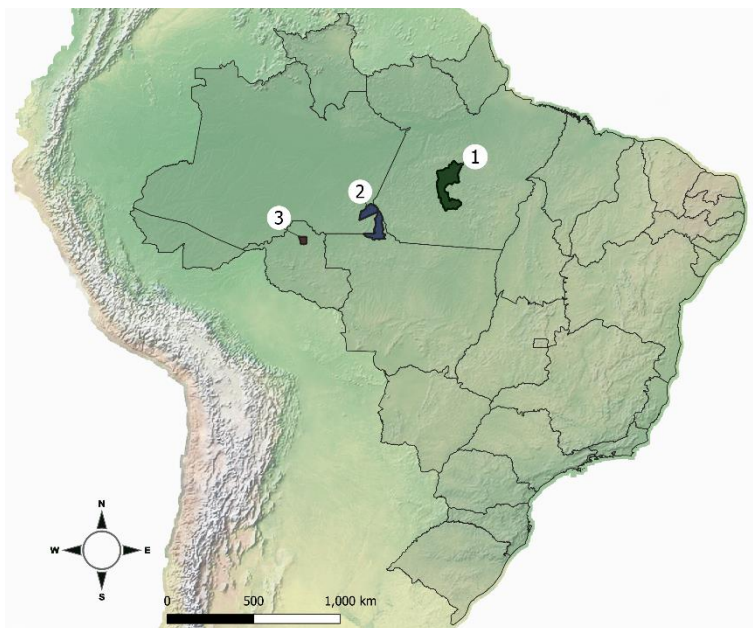## 2. Methods

2.1. Study site

Figure 1: Map over the three protected areas in which sampling occurred (Terra do Meio Ecological Station (1), Juruena National Park (2) and Jamari National Forest (3)) in relation to Brazil (shaded area). Black border lines show the states in Brazil. Background map derived from Natural Earth: www.naturalearthdata.com (Natural Earth, 2009 - 2021).

The camera trap surveys were performed in three protected areas (PAs) located in the Brazilian Amazon: Terra do Meio Ecological Station, Juruena National Park and Jamari National Forest (Fig. 1). All three have a tropical monsoon climate, with a mean annual temperature around 26ºC and annual rainfall of around 3,000 mm (Alvares et al., 2013). The dry season starts in June and ends in September, with a transition period between the dry and wet season from October to December (ARPA, 2011a; IBAMA, 2005a; ICMBio, 2015).

Terra do Meio Ecological Station, hereafter referred to as Terra do Meio (or TDM), was established in 2005 and is a strictly protected area, covering 3,373,111 hectares, in the state of Pará (within 4º10'00''S to 7º40'00''S and 52º70'00''W to 54º40'00''W; Appendix 1) (ICMBio, 2015). Being an Ecological Station, the main purpose of the PA is biodiversity

protection, therefore human access and activities are limited to educational and scientific purposes (ICMBio, 2015; Presidência da República (Brasil), 2000). Terra do Meio is surrounded by other PAs and indigenous lands, henceforth functioning as a core biodiversity area in this mosaic of conservation units (ICMBio, 2015; Ramos et al., 2016; Schwartzman et al., 2013). The camera trap survey site was located in undisturbed and secondary forest, in the Novo river basin within terra firme forest, meaning that the forest is not seasonally flooded (ICMBio, 2015).

Juruena National Park, hereafter referred to as Juruena (or PNJ) is a strictly protected area established in 2006 and covers 1,958,014 hectares (ARPA, 2011a). The national park lies in the northern region of Mato Grosso state and the south-eastern part of Amazonas state (6º90'00''S to 9º10'00''S and 57º70'00''W to 59º30'00''W; Appendix 2) (ARPA, 2011a; Dalponte et al., 2016). Juruena also borders other PAs and is part of the PA network in the southern Amazon (ARPA, 2011a). The camera traps were situated in the south-western region of the conservation unit in the Juruena and São João da Barra river basins. The forest at the survey site is terra firme rainforest, and the area is classified as a high priority for biodiversity conservation (ARPA, 2011b).

The National Forest of Jamari, hereafter referred to as Jamari (or JAM) is a sustainable use PA established in 1984, covering 222,156 hectares in the state of Rondônia (9º00'00''S to 9º30'00''S and 62º40'00''W to 63º10'00''W; Appendix 3) (IBAMA, 2005a; Pinage et al., 2016). Sustainable extraction of natural forest resources, including reduced impact logging (RIL) are allowed within National forests (IBAMA, 2005b; Presidência da República (Brasil), 2000). Jamari is divided into different zones according to the management objectives (IBAMA, 2005b). The camera traps were placed within a RIL concession area and in the adjoining conservation zone, which consist of terra firme forest with dense canopy cover (IBAMA, 2005a; Mestre et al., 2020; Pinage et al., 2016).

2.2. Data collection and management

2.2.1. Sampling methods

The camera trap surveys were part of the National Biodiversity Monitoring Program of *Instituto Chico Mendes de Conservação da Biodiversidade* (*Programa Monitora* ICMBio - Brazilian Ministry of the Environment), which is an in situ monitoring program of Federal Protected Areas in Brazil (de Oliveira Roque et al., 2018). Sampling followed the Tropical Ecology Assessment and Monitoring (TEAM) network standardised protocol for monitoring terrestrial vertebrates in tropical forests (Jansen et al., 2014; TEAM Network, 2011). In brief, cameras were placed at knee height (30-50 cm above ground) on suitable trees with the lens oriented to the north or south to reduce exposure from direct sunlight, and the vegetation around chosen trees was cleared to ensure a clear view from the camera lens (TEAM Network, 2011). Camera trap sites were not baited (Jansen et al., 2014; TEAM Network, 2011). The camera traps (Bushnell Trophy Cam HD) operated continuously for 24 hours per day and were set with

passive infrared sensors (Carvalho Jr et al., 2020; TEAM Network, 2011). This type of camera sensor system detects contrast in heat between a moving organism and the background environment (Meek et al., 2012; Rovero et al., 2010; Rovero et al., 2013; Swann et al., 2011). Colour photos were taken in light conditions and black and white images under poor light (TEAM Network, 2011). Camera traps were set at a trigger speed of 0.1 of a second and with high heat sensitivity (Jansen et al., 2014). Each camera was programmed to take three photos per trigger, to increase the likelihood of obtaining at least one good quality image (Jansen et al., 2014; Rovero et al., 2013; TEAM Network, 2011).

Sampling for this study occurred between June and December during 2016 in Terra do Meio and Juruena, and in 2018 in Jamari (Table 1). In Terra do Meio, camera traps were deployed in the dry season. Camera traps in Juruena were deployed in the transition period from dry to wet season, and in Jamari, sampling occurred both in the dry season and in the transition period to wet season.

In total, 235 camera traps were installed by ICMBio staff and volunteers. In Terra do Meio and Juruena, 60 camera traps were installed, whereas 115 were set up in Jamari. Cameras were placed in a predefined grid of arrays, where each array consisted of 20 to 30 camera traps at a density of one camera per 2 km^2 (TEAM Network, 2011). Camera trap arrays were deployed approximately simultaneously in Terra do Meio and Juruena. In Jamari, each array of camera traps operated sequentially due to limitations in the number of cameras. The total survey area covered by camera trap arrays was approximately 97 km^2, 108 km^2 and 418 km^2 in Terra do Meio, Juruena, and Jamari, respectively.

Camera traps, on average, operated for 57 (SE = 1.22), 35 (SE = 1.02), and 36 (SE = 1.43) days in Terra do Meio, Juruena, and Jamari, respectively (Table 1). Sampling effort was calculated by summing the number of trapping days per camera trap. The total sampling effort was 9,888 camera trap days.

TABLE 1: Sampling year and period, number of camera traps (No. CT), sampling-effort measured in number of camera trap days (CT-days), mean number of camera trap days per trap (Mean) and the standard error (SE) of the mean, and number of camera traps that stopped functioning within the first day (No.CT stop.) per site. (TDM: Terra do Meio, PNJ: Juruena, JAM: Jamari)

Site	Year	Period	No. CT	CT-days	Mean	SE	No. CT stop.
TDM	2016	Jun. – Aug.	60	3,483	57	1.22	0
PNJ	2016	Nov. – Dec.	60	2,185	35	1.02	1
JAM	2018	Aug. – Dec.	115	4,220	36	1.43	7

2.2.2. Data processing and species identification

All images were first processed in the wild.ID software by ICMBio staff or volunteers. This software uses artificial intelligence to assist in processing camera trap images (Ahumada et al., 2020; Fegraus et al., 2011; Thau et al., 2019). Data obtained from each image included: image ID, camera trap name, camera trap coordinates, photo type (Setup/pickup, animal

detection, unidentifiable photo, or unknown animal), photo date and time, species identity (including class, order, family, genus, and species), number of individuals per species recorded in each photo, and setup and pickup dates for each camera trap. Photos with multiple species had the same ID, but each species had a unique row in the datasets.

To minimise misidentification errors, I reprocessed images with avian detections. I also processed images where photo content was unknown to ensure that avian detections were not overlooked. Preidentified species were verified using identification guides (Delacour & Amadon, 2004; Perlo, 2009; Ridgely & Tudor, 1989; Ridgely & Tudor, 1994; WIKIAVES, n.d.) and unidentified species were identified when possible. In cases where species were unidentifiable, I identified the bird to the lowest taxonomic resolution possible (Order, Family and Genus). I followed the taxonomy list set by the Brazilian Ornithological Records Committee (de Piacentini et al., 2015). In photos where light quality was poor, images were treated to improve contrast and lighting using "*Microsoft Photos app*" (Windows 10). Images with uncertain or unknown identification were then sent to external experts for verification and identification.

Since several photographs were taken per detection and individuals tended to stay in front of the camera or move in and out of camera view, each photo could not be considered independent. Temporal independence of detections was assumed at a 60 minute interval, thus, only one species detection within an hour at a camera trap site was included for detection analysis (Sollmann, 2018). This 60-minute interval for temporal independence has been commonly used (Carvalho Jr et al., 2020; Dias et al., 2019; Griffiths et al., 2020; Pérez-Irineo & Santos-Moreno, 2021).

2.2.3. Species traits

Species traits included body mass (in grams) and foraging guild, which was defined by diet and foraging stratum. Body mass data were acquired from the EltonTraits database (Wilman et al., 2014). Information on foraging guild for identified birds was based on data from the EltonTraits database (Wilman et al., 2014) and Terborgh et al. (1990). For birds identified to genus, body mass was calculated taking the genus average, and diet and foraging stratum was based on what is typical within the genus, a method also used by Wilman et al. (2014). Birds not identified to species or genus level were excluded from the trait-based analysis.

Body mass

Based on body mass, species were categorised as small ($\leq$ 100g), medium ($100 > x \leq$ 600) and large (> 600; Appendix 4). Body mass may vary between sexes, geographically, seasonally, and during the day, but it is the most accurate and available variable to predict size (Dunning Jr, 2007). The body masses obtained from EltonTraits are based on the average across sexes provided by Dunning Jr. (2007) (Wilman et al., 2014). The size categories were defined by calculating the 0.25 quantiles of body mass estimated for the detected species in all

three sites. Species with body mass below the 0.25 quantile were classified as small, those between 0.25 and 0.75 were classified as medium, and species with a body mass higher than the 0.75 quantile were classified as large. The quantile estimates were rounded to the closest 100 grams for simplicity.

<u>Foraging guild</u>

Diet and foraging stratum were grouped to define the guild of the identified birds (Appendix 4). Based on avian diet terminology proposed by Lopes et al. (2016) and data from EltonTraits (Wilman et al., 2014) and Terborgh et al. (1990), the birds were grouped into six main dietary categories: granivores (Gr; seed-eaters), frugivores (Fr; fruit-eaters), insectivores (In; insect-eaters), raptors (Pr; predating all vertebrate species except for fish), scavengers (Sc; feeding on carcasses), and omnivores (Om; dietary generalists). Species were classified as omnivores when none of the five other categories were dominant - in other words, where more than two categories scored less than 50% or there was an equal ratio (50:50) of plant (frugivore and granivore) and animal (insectivore, raptor and scavenger) matter (Lopes et al., 2016; Wilman et al., 2014). Species feeding in aquatic environments were categorised as "aquatic", pooling species feeding on aquatic invertebrates and piscivores.

Information on the vertical forest stratum used by each forest species (non-aquatic) was obtained from EltonTraits (Wilman et al., 2014). Vertical foraging heights were divided into three main categories: terrestrial (T; ground-dwelling), understorey (U) and arboreal (A), which included midstorey and canopy dwellers (Appendix 4). If a species predominantly (more than 50% of the time) foraged within one stratum, this stratum was used to categorise the species. In cases where the proportion of foraging was equal (50:50) in two strata, both were used to classify the species. Species that occupied various foraging heights, but none of the strata were dominantly used, were defined as "forest stratum generalists" (TUA).

2.3. Statistical analysis

2.3.1. Rarefaction and species richness

Rarefaction analysis was used for standardised comparison of detected species richness between sites. Through rarefaction, sample size at each site was normalised to the lowest number of detections and, species richness was subsequently estimated at this standard sample size and compared between sites (Eqn. 1) (Chao et al., 2014; Gotelli & Colwell, 2001; Hurlbert, 1971; Oksanen, 2020).

Equation 1: Rarefaction function, predicting the expected species richness at the normalised sample size, where n is the smallest detected sample size from the three sites, N is the actual detected sample at each site, and S is the number of detected species (Hurlbert, 1971).

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\left(\frac{N - N_i}{n} \right)}{\left(\frac{N}{n} \right)} \right]$$

Species richness was defined as the number of distinct species detected (Hurlbert, 1971). Detections of individuals not identified to species level were therefore excluded from the rarefaction analysis. Rarefaction curves were used to determine whether observed species richness at each site was affected by sample size (number of independent detections) or sampling effort (camera trap days) (Oksanen, 2020). The '*vegan*' package in R was used to perform rarefaction analysis (Oksanen et al., 2020).

2.3.2. Detection rate in relation to body mass

I created negative binomial regression models with a log link function to analyse whether body mass affected detection rate. Negative binomial regression models were used to compensate for the overdispersion (mean was not equal to variance) in the count data (Dunn & Smyth, 2018; Hoffmann, 2016). Both the response variable (number of detections) and explanatory variable (body mass) were $\log_{10}$ transformed, since the distribution of species was clustered at low body mass and detection rates of certain species were low.

2.3.3. Diel activity analysis

To determine when birds were most active (i.e. whether detections occurred during the day, night, or twilight hours (crepuscular period)), I obtained time of sunrise, sunset, start of nautical twilight at dawn, and end of nautical twilight at dusk, for each camera trap location on each photo date using the '*suncalc*' package in R (Thieurmel & Elmarhraoui, 2019). The crepuscular period was defined as the time in which the sun is positioned between 0 (sunrise/sunset) and 12 degrees below the horizon, which includes both the nautical (sun position: 6-12º below horizon) and civil (sun position: 0-6º below horizon) twilight (Daan & Aschoff, 1975; Ensing et al., 2014; Hertel et al., 2016; Quispe et al., 2017). Night was defined as lasting from the end of nautical dusk to the start of nautical dawn and the time between sunrise and sunset were defined as day (Ensing et al., 2014).

Average double anchoring

Due to large distances between sites on an east-west axis, the easternmost site (Terra do Meio) lies in a different time zone (GMT-3) to the two other sites (GMT-4). I, therefore, had to adjust for differences in sunrise and sunset time and daylength. If these variations were not considered, activity level may be under- or overestimated and time of activity misinterpreted (Nouvellet et al., 2012; Rowcliffe et al., 2014; Vazquez et al., 2019). Sunrise and sunset time and daylength for each detection date and camera trap location was obtained using the '*suncalc*' package (Thieurmel & Elmarhraoui, 2019). A Kruskal-Wallis test showed that daylength differed significantly between sites ($H(2) = 2351.7$, $p < 0.001$). Due to variations in daylength and sunrise and sunset time, local time could not be used for unbiased comparisons between activity patterns observed at the three sites (Rowcliffe et al., 2014; Vazquez et al., 2019). Instead, average double anchoring was used, where the time of detection was transformed to solar time, anchoring the time to the average sunset and sunrise of the three sites within the study periods (06:22 sunrise and 18:26 sunset; Eqn. 2) (Vazquez et al., 2019). The

transformation of local time to the double anchored solar time in radians was carried out using the "solartime" function in the '*activity*' package in R (Rowcliffe & Rowcliffe, 2019).

Equation 2: Average double anchoring function, where T_d is the double anchored time of activity, T_c is the local clock time of activity, Z_1 and Z_2 are the local time of sunrise and sunset of the day of detected activity and $\dot{Z}_1$ and $\dot{Z}_2$ are the anchor times (Vazquez et al., 2019).

$$T_d = \dot{Z}_1 + (\dot{Z}_2 - \dot{Z}_1)\frac{T_c - Z_1}{Z_2 - Z_1}$$

Estimating diel activity patterns

Diel activity pattern analyses were executed for all detections per site, for the four most common (> 100 detections) families (Tinamidae, Psophiidae, Cracidae, and Columbidae) and for vertical foraging height categories with the most frequently detected species (terrestrial, arboreal, and foraging strata generalists). Although sample sizes below 100 individuals are proposed adequate for estimating activity patterns (Ridout & Linkie, 2009), a sample size of 100 detections is recommended for reduced estimation errors (Lashley et al., 2018). Therefore, activity patterns were only analysed for functional groups with a sample size of at least 100 detections, and comparisons between sites were only executed if this criterion was fulfilled at all three sites.

The diel activity of each specified group was estimated using nonparametric kernel density estimation. The kernel density function estimates the density of detections across a 24-hour circular scale without categorising data into time intervals (Frey et al., 2017; Silverman, 1986). Nonparametric statistics were used to hinder assumptions of the distribution family of the data when calculating the probability density functions (Clemons & Bradley Jr, 2000; Silverman, 1986). The kernel density estimator is derived from the probability density function fitted to the detection times observed in the data, and the angular distance between a random point and detection points in the data (Eqn. 3) (Oliveira-Santos et al., 2013; Ridout & Linkie, 2009; Rowcliffe et al., 2014).

Equation 3: Function estimating the kernel density, where K_v is the probability density function at smoothing parameter v and d is the angular distance between detections (Ridout & Linkie, 2009; Taylor, 2008).

$$\hat{f}(x; v) = \frac{1}{n}\sum_{i=1}^{n} K_v[d(x, x_i)]$$

The bandwidth, also known as the smoothing parameter, directly influences the kernel density function. Underestimating the smoothing parameter results in narrow spiking activity peaks, whilst overestimating creates shallow peaks with detail reduction (Clemons & Bradley Jr, 2000; Oliveira-Santos et al., 2013; Silverman, 1986; Taylor, 2008). For the current study,

the smoothing parameter was set to 3 as proposed by Ridout and Linkie (2009), who found that at this value the main characteristics of the activity distributions were maintained.

The '*overlap*' package in R was used to plot fitted kernel densities of activity (Meredith et al., 2020). Probability density functions and activity levels were estimated using the '*activity*' package in R (Rowcliffe & Rowcliffe, 2019). The activity level was estimated using the method proposed by Rowcliffe et al. (2014) and is defined as the ratio between the amount of time allocated to activity (area under the activity curve) and the area created if the focal population stayed continuously active throughout 24-hours at the highest activity level detected (Eqn. 4). Standard errors and confidence intervals on the activity level estimate were derived using 200 bootstrap samples (Clemons & Bradley Jr, 2000; Rowcliffe et al., 2014).

Equation 4: Function estimating activity level, where f_{max} is the probability density function at the highest peak of activity with a value between 0 and 2π as detection times are converted to radian time (Rowcliffe et al., 2014).

$$p = \frac{1}{2\pi f_{max}}$$

The Wald test (Eqn. 5) was used to figure out whether activity level estimates differed significantly between sites and focal groups, using the "*compareAct*" function in the '*activity*' package (Rowcliffe et al., 2014; Rowcliffe & Rowcliffe, 2019).

Equation 5: The Wald test function, where E_i are the compared kernel density (activity) estimates and s_i are the standard errors of E_i, respectively (Rowcliffe et al., 2014; Wald, 1943).

$$W = \frac{(E_1 - E_2)^2}{s_1^2 + s_2^2}$$

Further, the overlap of diel activity patterns was estimated using Ridout and Linkie's (2009) coefficient of overlap (Δ) using the "*overlapEst*" function in the '*overlap*' package (Meredith et al., 2020). The coefficient of overlap is the area where two probability densities overlap and obtained values lie between 0 and 1, where $\Delta = 0$ if no overlap occurs and $\Delta = 1$ when activity density estimates are equal (Clemons & Bradley Jr, 2000; Ridout & Linkie, 2009; Schmid & Schmidt, 2006). The $\widehat{\Delta_4}$ function was used to estimate Δ, as sample size for the analysed groups was greater than 75 (Eqn. 6) (Meredith et al., 2020; Ridout & Linkie, 2009; Schmid & Schmidt, 2006). Coefficient of overlapping estimates were categorised into low, moderate and high overlap with respective thresholds; $\Delta \leq 0.5$, $0.5 < \Delta \leq 0.75$, and $\Delta > 0.75$ (Marinho et al., 2020).

Equation 6: *Function estimating the coefficient of overlap ($\widehat{\Delta_4}$ as sample size of the smallest sample was >75), where T is number of equally spaced times, t_i is a set of equally spaced times in radians, x_i and y_i are two sets of sample times of sample size n and m, respectively (Meredith et al., 2020; Ridout & Linkie, 2009; Schmid & Schmidt, 2006).*

$$\widehat{\Delta_4}= \frac{1}{2}\left(\frac{1}{n}\sum_{1=1}^{n} \min\left\{1,\frac{\hat{g}(x_i)}{\hat{f}(x_i)}\right\} + \frac{1}{m}\sum_{1=1}^{m} \min\left\{1,\frac{\hat{f}(y_i)}{\hat{g}(y_i)}\right\}\right)$$

All analyses were executed using the integrated development environment RStudio in the statistical software R (version 4.0.1) (RStudio Team, 2020).

3. Results

3.1. Detections and species richness

A total of 53,546 bird images were captured (Terra do Meio: 34,237; Juruena: 13,471 and Jamari: 5,838). The one-hour interval threshold for temporal independence produced a total of 4,134 independent detections (Terra do Meio: 2,793; Juruena: 703 and Jamari: 638). Most detections (87.4%) were identified to species, and only seven detections (0.2%) could not be identified to order (Table 2).

Table 2: *Number (No. det) and percentage (%) of independent detections identified to species-, genus-, family-, order-, and class level (identified to class level means that a bird was detected, but order could not be identified).*

Taxonomic level	Terra do Meio		Juruena		Jamari		Total	
	No. det	%	No. det	%	No. det	%	No. det	%
Species	2,352	84.2	659	93.7	603	94.5	3,614	87.4
Genus	122	4.4	39	5.5	17	2.7	178	4.3
Family	307	11.0	5	0.7	15	2.4	327	7.9
Order	8	0.3	-	-	-	-	8	0.2
Class	4	0.1	-	-	3	0.5	7	0.2

In total, 66 species from 51 genera, 31 families, and 16 different orders were registered (Appendix 4). Overall, 22 of these species were only detected once. Tinamidae, Psophiidae, Cracidae, Columbidae, and Formicariidae were the five most abundant families while *Mitu tuberosum, Psophia dextralis, Leptotila rufaxilla, Tinamus major,* and *Psophia viridis* were the five most abundant species. Terra do Meio had the highest number of identified species (53), followed by Juruena (33), and Jamari (20). The most common species detected in Terra do Meio was *P. dextralis* with 393 independent detections, followed by 307 detections of *M. tuberosum. M. tuberosum* was the most recorded species in Juruena (236 detections) and Jamari (208 detections). The second most common species in each case was *L. rufaxilla* (98 detections) in Juruena and *P. viridis* (127 detections) in Jamari.

The rarefaction curves differed between sites (Fig. 2). In Terra do Meio, the curve was still increasing after 2000 detections although the species accumulation rate started to decrease

after 500 detections (Fig. 2 a). In Juruena and Jamari, the sample size (in terms of independent detections) was relatively small and still accumulating species at a high rate (Fig. 2 a). However, fewer species seemed to be accumulated at both these sites than at Terra do Meio, particularly at Jamari. In fact, the predicted species richness for each site after being rarefied to the smallest sample size (603 in Jamari) was 39.7 (SE = 2.18), 31.6 (SE = 1.11), and 20.0 (SE = 0.0) in Terra do Meio, Juruena, and Jamari, respectively.

Jamari had the highest sampling effort in terms of camera trap days (4,220 days), but had the lowest species richness (Fig. 2 b). Jamari accumulated species at a lower rate and the curve is approaching an asymptote, whereas in Terra do Meio and Juruena, species were continuing to accumulate at a higher rate (Fig. 2 b). Sampling effort was lowest in Juruena (2,185 days), at which point this site seemed to be accumulating species at the highest rate, although the total species richness observed was still significantly lower than at Terra do Meio.
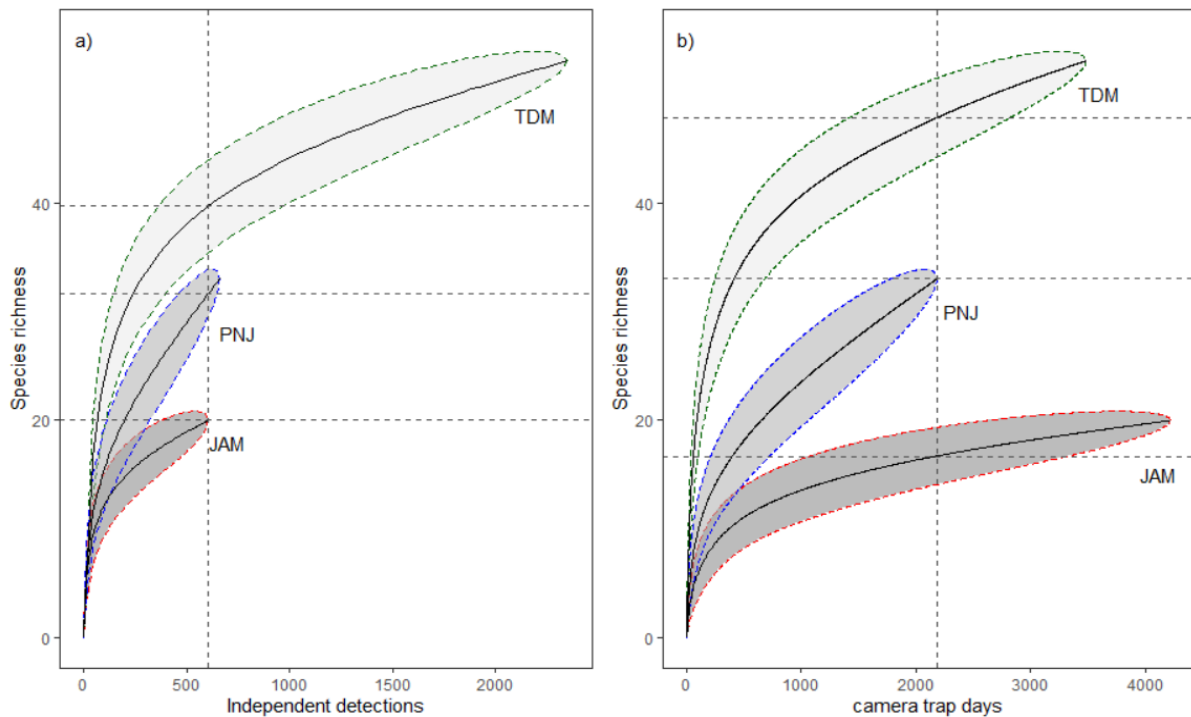
Figure 2: *Individual-based (a) and sample-based (b) rarefaction curves for Terra do Meio (TDM – green), Juruena (PNJ – blue) and Jamari (JAM – red), where solid black lines are the rarefaction curves and the grey zones with dotted line borders are the 95% confidence intervals (CI) for each site.* **a**) *Detected species richness against number of independent detections, where the dashed grey horizontal lines show predicted species richness at the smallest sample size (603 – JAM; vertical line) to which sample size from each site is rarefied (TDM: 39.7 spp.; SE = 2.18, PNJ: 31.6 spp.; SE = 1.11, JAM: 20 spp.; SE = 0.0).* **b**) *Detected species richness against camera trap days (CT-days) per site (TDM: 53 spp., 3,483 CT-days; PNJ: 33 spp., 2,185 CT-days; JAM: 20 spp., 4,220 CT-days), where horizontal dashed grey lines represent predicted species richness at the lowest sampling effort (2,185 days – PNJ; TDM: 47.8 spp., SE = 3.62, PNJ: 33 spp., SE = 0.0, JAM: 16.7 spp., SE = 2.63).*

3.2. Notable findings

Nothocrax urumutum

The extremely secretive Nocturnal curassow (*Nothocrax urumutum*) was detected four times in total; once in Juruena and three times in Jamari. All records were from early to late morning (05:55h -11:17h). In Juruena, three individuals were detected (Fig. 3 a) together with one *M. tubersosum* individual (Fig. 3 b). In Jamari, all three detections were of two individuals.

Figure 3*: a) Three Nothocrax urumutum caught on camera on the 7th December 2016 between 09:07 to 09:15 (GMT-4) in Juruena National Park (Lat.: -8.95788, Long.: -58.6172) b) Mitu tuberosum (back right) was detected together with N. urumutum two minutes after the first Nothocrax detection.*

Neomorphus squamiger

The shy, secretive, and rarely observed Scaled-ground cuckoo (*Neomorphus squamiger*) was detected ten times in Terra do Meio with one individual per detection (Fig. 4). The species was detected during the day between 09:47h and 14:26h, on ten different days. Detections were recorded at nine different camera trap sites distributed across the entire survey area.

Figure 4: *Neomorphus squamiger detected on the 7th July 2016 at 10:49 (GMT-3; Lat.: -4.73557, Long.: -53.5438) in Terra do Meio*

3.3. Species traits

Body mass

The smallest species detected was *Hylophylax punctulatus* with an average body mass of 12.4g. The largest detected species was *M. tuberosum* with an average body mass of 2,769.5g. Most species detected were classified as small (27) or medium-sized (23), while 16 species were large (Table 3). However, large species were most frequently recorded (2,240 independent detections), followed by 1,255 detections of medium species, and 297 independent records of small species (Table 3). In fact, body mass had a significant positive effect on detection rate (GLM: z-value = 3.44, $p < 0.001$), as smaller species were less detected than species with higher body mass (Fig. 5). The log-log relationship between number of detections per species and body mass was non-linear; the predicted detection rate was higher for larger-bodied species (Fig. 5).

Table 3: *Number of independent detections (No. det) and identified species (No. spp; genus (in parenthesis) when species was not identified) within each size category for each site and in total.*

Body size	Terra do Meio		Juruena		Jamari		Total	
	No. det	No. spp	No. det	No. spp	No. det	No. spp	No. det	No. spp
Small (≤100g)	287	25 (3)	8	6 (1)	2	2 (0)	297	27 (3)
Medium (>100g & ≤ 600g)	909	17 (2)	197	12 (3)	149	9 (2)	1,255	23 (3)
Large (> 600g)	1,278	11 (2)	493	15 (1)	469	9 (2)	2,240	16 (2)
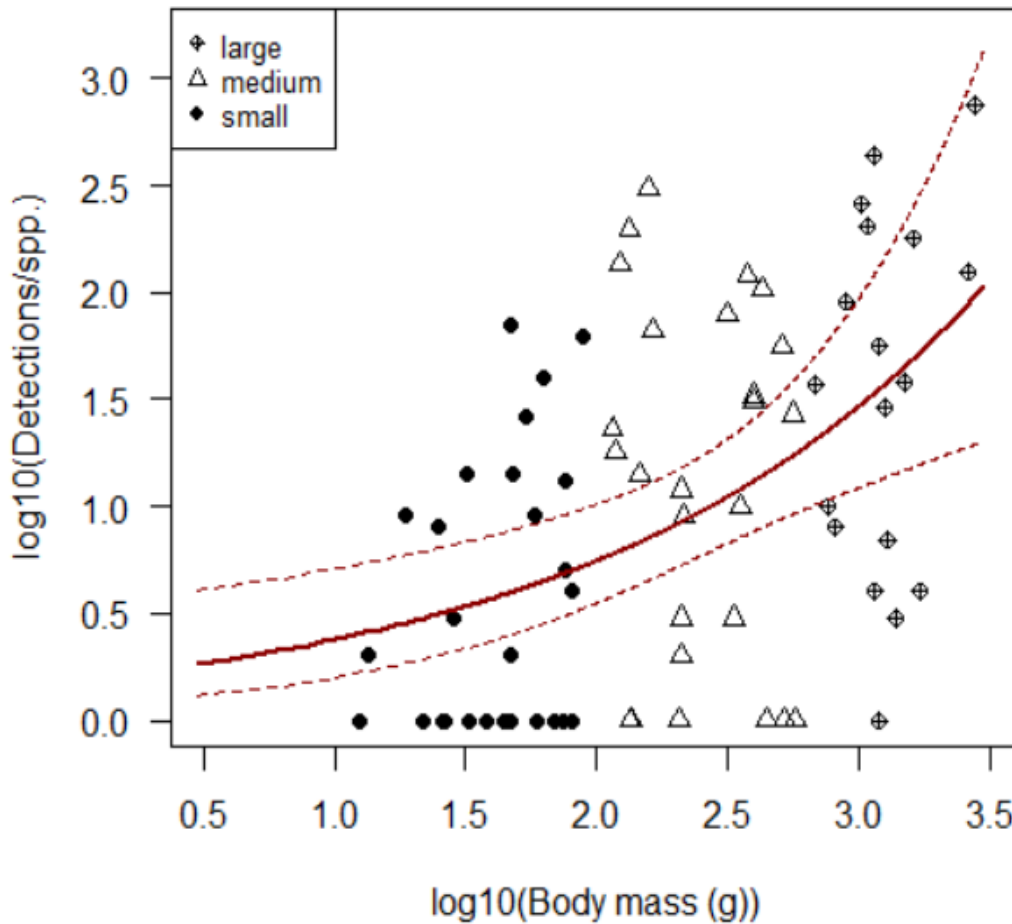
Figure 5: *Relationship between number of detections per species and body mass (g). Both the response and explanatory variables are in the common logarithm scale (log₁₀). The fitted line (dark red) is the predicted relationship between the two variables, using a negative binomial regression model with log link function: $\log_{10}(detections) \sim \log_{10}(body\ mass)$. The 95% confidence intervals of the prediction line are represented with dashed lines. Each data point represents a species (or genus when individuals were not identified to species), with body size category represented by symbol type (small; filled circle, medium; triangle, and large; circle with cross)*

Terrestrial frugivores were most frequently detected (1,762), followed by 732 independent detections of terrestrial omnivores (Table 4). Most species detected were terrestrial insectivores (15), followed by terrestrial frugivore species (10). Six guilds only contained one species. Terrestrial frugivores were most frequently detected at all three sites. Terrestrial omnivores were second most detected in Terra do Meio, whereas terrestrial granivores were second most detected in Juruena and Jamari (Table 4). The highest number of terrestrial insectivorous species was detected in Terra do Meio (14), whereas only two and one species within this guild were detected in Juruena and Jamari, respectively.

Table 4: *Number of independent detections (No. det) and identified species (No. spp; genus (in parenthesis) when species was not identified) for each guild within each site and in total.*

Guild	Terra do Meio		Juruena		Jamari		Total	
	No. det	No. spp	No. det	No. spp	No. det	No. spp	No. det	No. spp
TERRESTRIAL								
Granivore	317	3 (1)	161	3 (1)	106	1 (1)	584	3 (1)
Frugivore	968	8	398	9	396	7	1,762	10
Insectivore	325	14 (1)	2	2	1	1	328	15 (1)
Predator	1	1	-	-	-	-	1	1
Scavenger	2	1	1	1	-	-	3	1
Omnivore	557	5 (3)	92	4 (3)	83	4 (2)	732	7 (3)
TER./UND.[1]								
Insectivore	8	1	-	-	1	1	9	1
Omnivore	13	2	-	-	-	-	13	2
UNDERSTOREY								
Predator	1	1	-	-	1	1	2	1
Omnivore	13	1	1	1	-	-	14	1
ARBOREAL								
Frugivore	118	2 (1)	21	3	27	2 (1)	166	4 (1)
Insectivore	6	4	2	2	-	-	8	6
Predator	-	-	1	1	3	1	5	2
Omnivore	-	-	1	1	1	1	1	1
TER./UND./ARB.[2]								
Insectivore	97	6 (1)	4	3	-	-	101	6 (1)
Predator	-	-	1	0 (1)	-	-	1	0 (1)
AQUATIC[3]	48	4	13	3	1	1	62	5

[1] *Terrestrial/Understorey*
[2] *Terrestrial/Understorey/Arboreal – foraging stratum generalist*
[3] *Aquatic invertebrate eaters and piscivores pooled*

3.4. Diel activity patterns

At each site, the highest number of detections occurred during the day (3,824; 92.5% of all detections; Table 5; Fig. 6). These detections comprised 65 species and 422 bird detections not identified to species (Appendix 4). The only species not recorded during the day was Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), which was only detected once at night. During twilight, 210 detections (5.1%) occurred with 28 species recorded and 29 bird detections not identified to species. The lowest number of detections occurred during the night with a total of 100 records (2.4%) from 11 distinct species. From the 100 night-time detections, 69 were unidentifiable to species within Columbidae and Tinamidae.
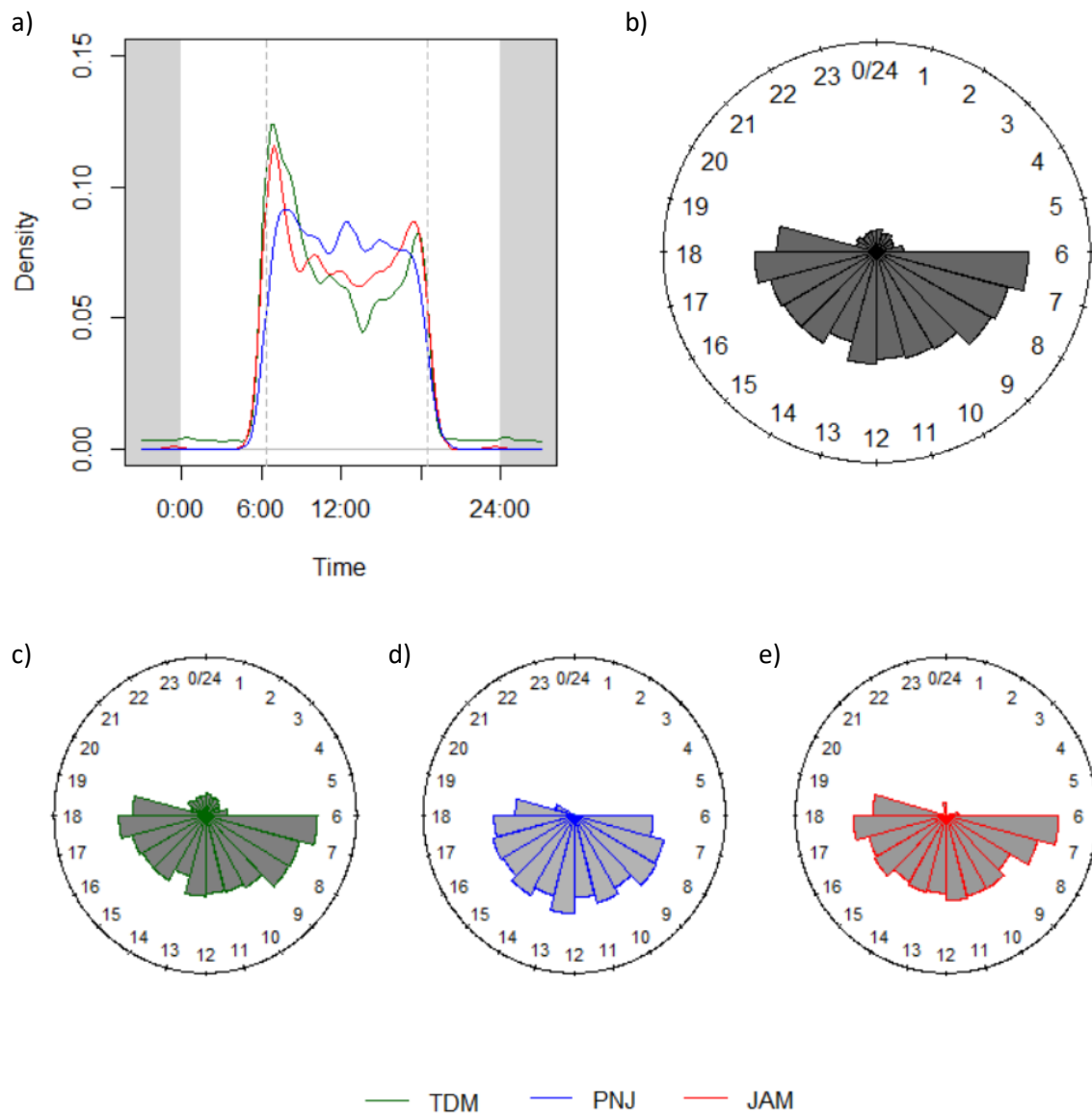
Figure 6: Diel activity patterns displayed as (a) Kernel density plot of estimated activity for all independent detections recorded at each site (TDM: Terra do Meio, green; PNJ: Juruena, blue; JAM: Jamari, red), and circular plots depicting the relative frequency of detection events divided into hour periods on a square root scale for (b) all sites combined, and for (c) Terra do Meio, (d) Juruena, and (e) Jamari separately. Solar time was anchored to average sunrise (06:22) and sunset (18:26), shown as dashed vertical lines in (a).

Table 5: *Number of independent records detected (No. det) and percentages (%) during twilight (dawn and dusk), day (sunrise till sunset), and night (end of nautical dusk till start of nautical dawn), for each site and in total. Percentages are calculated based on the total number of detections per site.*

Diel period	Terra do Meio		Juruena		Jamari		Total	
	No. det	%	No. det	%	No. det	%	No. det	%
Twilight (dawn)	137	4.9	2	0.3	13	2.0	152	3.7
Day	2,514	90.0	694	98.7	616	96.6	3,824	92.5
Twilight (dusk)	43	1.5	7	1.0	8	1.3	58	1.4
Night	99	3.5	0	0	1	0.2	100	2.4

In Terra do Meio, activity was recorded throughout the 24-hour cycle (Table 5; Fig. 6 c). During the night, unidentified Columbidae species were most common (67 detections), followed by 16 Tinamidae records. *Chamaeza nobilis* had the highest number of detections (72) during twilight (Appendix 4). There were no avian records during the night in Juruena and only nine detections during twilight (Table 5; Fig. 6 d). In Jamari, only one species (*Geotrygon montana*) was detected during the night (Table 5; Fig. 6 e).

The number of detections peaked during sunrise and sunset in Terra do Meio and Jamari, with the highest peak being at sunrise (Fig. 6 a, c, e). In Juruena, the first activity peak occurred in the second and third hour after sunrise (Fig. 6 a, d). The activity pattern in Juruena was significantly different from Terra do Meio (Wald test: W = 23.33, p < 0.001) and Jamari (W = 12.54, p <0.001), whereas Terra do Meio and Jamari did not differ significantly (W = 0.001, p = 0.98; Table 6 a). Although there were significant differences between Juruena and the two other sites, the coefficient of overlap between all sites was high (Δ > 0.75), showing that overall, activity patterns between sites overlapped greatly and were quite similar.

In general, the activity of the four most common families detected at each site (Tinamidae, Psophiidae, Cracidae, and Columbidae) was highest at sunrise and sunset. Activity depressions and minor peaks were observed during the day and low levels of activity during the night (Fig. 7). Tinamids followed this pattern and did not differ significantly between sites (Table 6 b; Fig. 7 a). For Psophiidae and Cracidae, detections were more constant throughout the day (Fig. 7 b, c) - except for cracids detected in Terra do Meio, where detections peaked at sunrise and were much lower in the afternoon than at the two other sites (Fig. 7 c). In fact, cracid activity in Terra do Meio differed significantly from Juruena and Jamari (W = 7.42 and 7.34, respectively; p = 0.01; Table 6 d). Activity in Psophiidae was also significantly different between Terra do Meio and Juruena (W = 7.22; p = 0.01; Table 6 c). Despite the significant differences between sites for activity patterns within Psophiidae and Cracidae, the coefficient of overlap was high (Δ > 0.75), showing an overall similarity in activity (Table 6 c, d). Within Columbidae, differences in activity patterns between sites were more apparent (Fig. 7 d). Columbidae detections in Jamari were higher during sunrise and lower during midday and therefore differed significantly from Terra do Meio and Juruena (W = 44.04 and 33.53 respectively; p < 0.001) with a moderate level of overlap (Δ = 0.69 and Δ = 0.59 respectively;

Table 6 e). Columbidae activity in Juruena was skewed towards noon, with lower activity levels at sunrise and sunset than at mid-day (Fig. 7 d).

a)

Tinamidae

b)

Psophiidae

c)

Cracidae

d)

Columbidae

TDM   PNJ   JAM
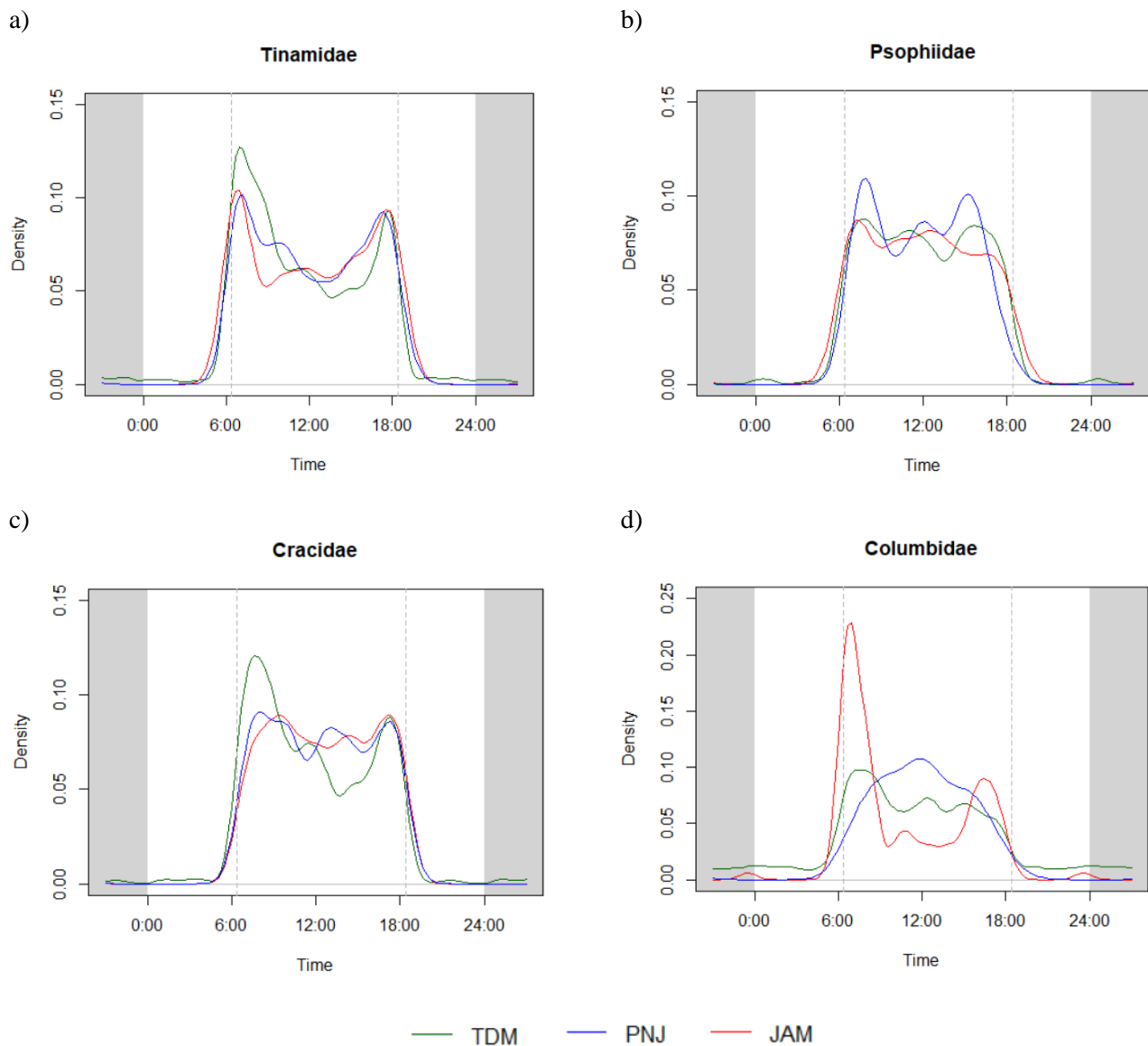
Figure 7: *Kernel density plots of diel activity patterns of the four most common (>100 independent detections) families (Tinamidae (a), Psophiidae (b), Cracidae (c) and Columbidae (d)) detected at each site (TDM: Terra do Meio, green; PNJ: Juruena, blue; JAM: Jamari, red). Solar time was anchored to average sunrise (06:22) and sunset (18:26), shown as dashed vertical lines.*

Terrestrial species were most active at sunrise and sunset with lower detection rates during the day (Fig. 8 a). The activity of arboreal species and foraging strata generalists was skewed towards noon (Fig. 8 b, c). Activity patterns for terrestrial and arboreal species differed significantly (W = 7.52, p = 0.01; Table 6 g). However, the coefficient of overlap between these three vertical foraging strata was high ($\Delta > 0.75$; Table 6 g).

Comparing activity patterns within terrestrial species between sites showed differences between Juruena and the two other sites (Fig. 8 a). Terrestrial species in Juruena deviated from the general trend of high activity at sunrise and sunset, with lower activity at mid-day. Instead, they were more constantly detected throughout the day with less distinct activity peaks. The activity of terrestrial species in Juruena was, therefore, significantly different from that in Terra do Meio and Jamari (W = 24.22, p < 0.001 and W = 9.60, p < 0.01, respectively; Table 6 f).

a)

b)

c)
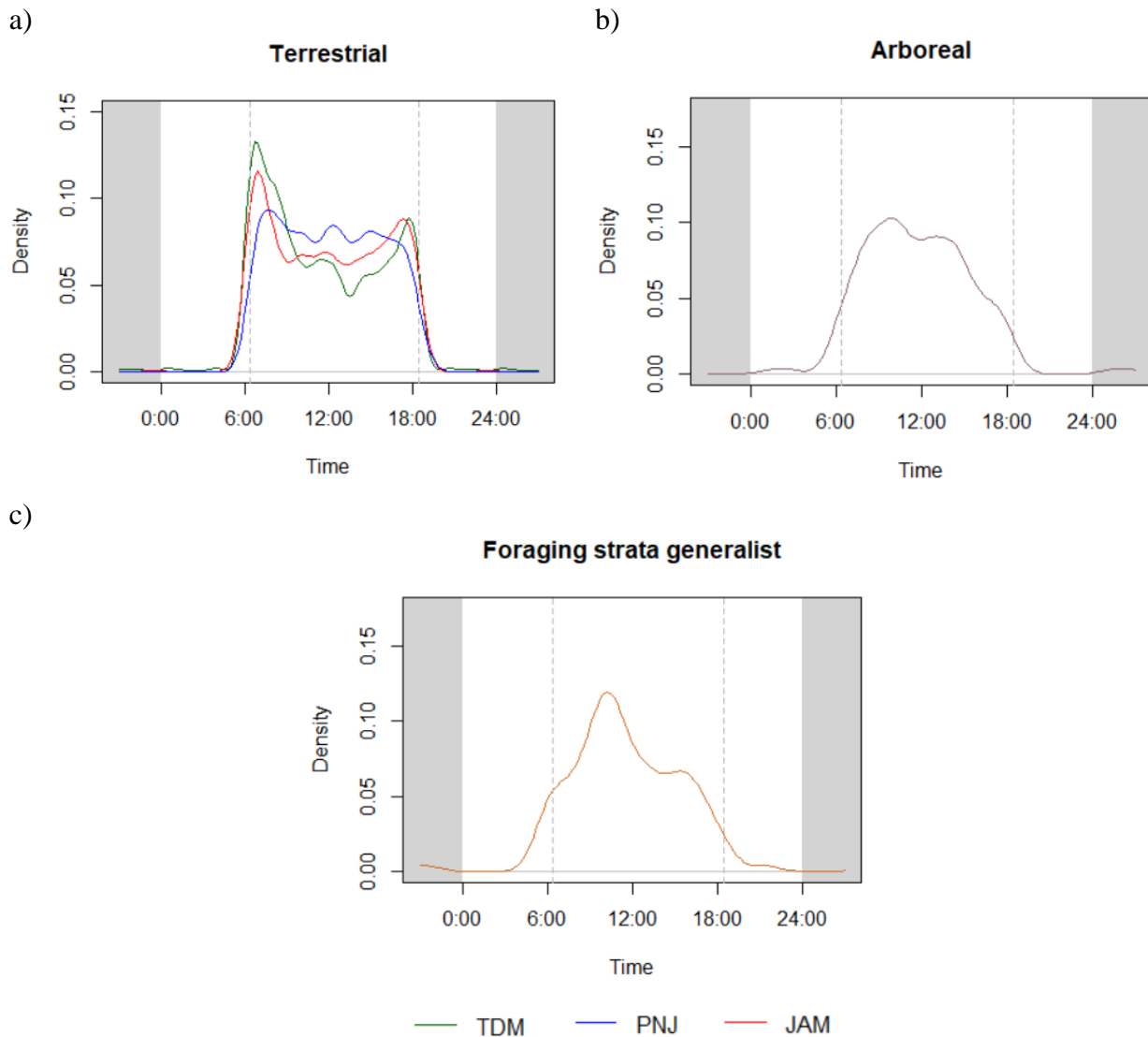
Figure 8: Kernel density plots of diel activity patterns for the most frequently detected (>100 independent detections) foraging strata: (a) Terrestrial species, (b) Arboreal species (including midstorey and canopy dwellers), and (c) foraging strata generalists (foraging at ground, understorey, midstorey and canopy). Activity patterns were estimated per site for terrestrial species (TDM: Terra do Meio, green; PNJ: Juruena, blue; JAM: Jamari, red), whereas all sites were combined for arboreal and foraging strata generalists due to a limited sample size. Solar time was anchored to average sunrise (06:22) and sunset (18:26), shown as dashed vertical lines.

Table 6: *Sample size (No. det), activity level estimates including standard error (SE) and 95% confidence intervals (CI), and statistical differences between activity level estimates (using Wald test and estimating coefficient of overlap (Δ; $\hat{\Delta}_4$ as sample sizes were > 75)) for (a) all independent detections, (b- e) the four most common families, (f) terrestrial species, and (g) the most frequently detected vertical foraging heights. Testing for statistical differences in a – f was done between sites (TDM: Terra do Meio; PNJ: Juruena; JAM: Jamari), and in g between foraging strata categories (T: Terrestrial, TUA: Terrestrial/Understorey/Arboreal (forest strata generalists), A: Arboreal). P-values < 0.05 are in bold representing significant difference.*

	No.det	Activity level [1] Est.	SE	CI		Wald test Dif.	SE	W	P	Δ $\hat{\Delta}_4$
a) All independent detections										
TDM	2793	0.31	0.02	0.31 – 0.37	*TDM vs PNJ*	-0.14	0.03	23.33	**< 0.001**	0.85
PNJ	703	0.44	0.02	0.38 – 0.47	*TDM vs JAM*	0.001	0.04	0.001	0.98	0.92
JAM	638	0.31	0.03	0.30 – 0.42	*PNJ vs JAM*	-0.14	0.04	12.54	**< 0.001**	0.90
b) Tinamidae										
TDM	632	0.29	0.02	0.25 – 0.33	*TDM vs PNJ*	-0.04	0.05	0.60	0.44	0.90
PNJ	118	0.33	0.05	0.23 – 0.42	*TDM vs JAM*	-0.02	0.05	0.10	0.75	0.90
JAM	150	0.30	0.04	0.22 -0.38	*PNJ vs JAM*	-0.02	0.06	0.15	0.70	0.94
c) Psophidae										
TDM	393	0.46	0.03	0.35 – 0.46	*TDM vs PNJ*	0.13	0.05	7.22	**0.01**	0.90
PNJ	121	0.33	0.04	0.25 – 0.39	*TDM vs JAM*	0.05	0.05	0.92	0.34	0.95
JAM	127	0.41	0.04	0.31 – 0.45	*PNJ vs JAM*	0.08	0.05	2.14	0.14	0.89
d) Cracidae										
TDM	614	0.40	0.03	0.33 – 0.44	*TDM vs PNJ*	-0.10	0.04	7.42	**0.01**	0.89
PNJ	161	0.36	0.03	0.28 – 0.39	*TDM vs JAM*	-0.11	0.04	7.34	**0.01**	0.88
JAM	109	0.15	0.02	0.11 – 0.21	*PNJ vs JAM*	0.005	0.04	0.01	0.91	0.96
e) Columbidae										
TDM	614	0.40	0.03	0.33 – 0.44	*TDM vs PNJ*	0.04	0.04	0.93	0.33	0.80
PNJ	161	0.36	0.03	0.28 – 0.39	*TDM vs JAM*	0.25	0.04	44.04	**< 0.001**	0.69
JAM	109	0.15	0.02	0.11 – 0.21	*PNJ vs JAM*	-0.21	0.04	33.52	**< 0.001**	0.59
f) Terrestrial										
TDM	2170	0.28	0.01	0.26 – 0.31	*TDM vs PNJ*	-0.14	0.03	24.22	**< 0.001**	0.84
PNJ	654	0.43	0.03	0.35 – 0.45	*TDM vs JAM*	-0.02	0.03	0.54	0.46	0.92
JAM	586	0.31	0.03	0.26 – 0.37	*PNJ vs JAM*	-0.12	0.04	9.60	**0.002**	0.89
g) Vertical foraging strata										
T	3410	0.30	0.01	0.27 – 0.32	*T vs TUA*	-0.03	0.05	0.32	0.57	0.80
TUA	102	0.32	0.05	0.24 – 0.42	*T vs A*	-0.09	0.03	7.52	**0.01**	0.80
A	180	0.39	0.03	0.29 – 0.42	*A vs TUA*	0.07	0.06	1.44	0.23	0.92

[1] *Activity level is estimated on the ratio between the detected time of activity and the maximum probability density function if the focal population remained continuously active at the highest level of activity for the whole diel cycle (Rowcliffe et al., 2014).*

4. Discussion

4.1. Species richness

The sampling conducted in this study yielded 66 identified bird species (range 20-53) across the three sites. This was higher than the avian species richness detected by ground-based camera traps in other studies in the Amazon conducted to date, which ranged between 4 and 17 (Blake et al., 2017; Carvalho Jr et al., 2020; Costa et al., 2018; Mere Roncal et al., 2019; Paredes et al., 2017). However, non-terrestrial and smaller sized species were excluded in most of these studies (Blake et al., 2017; Carvalho Jr et al., 2020; Costa et al., 2018; Mere Roncal et al., 2019), or specific dietary guilds were targeted (Paredes et al., 2017). Direct comparisons are, therefore, difficult.

A respectable 87.4% of the independent detections in this study were identified to species level, confirming that camera trap image quality is sufficient to identify many avian species. This has been asserted by previous research (Mere Roncal et al., 2019; Murphy et al., 2018; Santos-Moreno et al., 2019). Camera traps therefore appear to be a useful tool for detecting and gathering natural history information about a suite of cryptic, rare, or little-known terrestrial avian species (Kays et al., 2010; O'Brien & Kinnaird, 2008; Silveira et al., 2003). This is underlined by several detections of elusive species in the families, Tinamidae and Odontophoridae, and notable detections of two little-known species (*Nothocrax urumutum* and *Neomorphus squamiger*) in the current study. These results also suggest that there is a huge amount of untapped and ignored camera trap footage that would yield important avian detections for ecological and conservation purposes among the camera trap surveys that have been, or are currently being, conducted in tropical forests worldwide (Steenweg et al., 2017). For example, *Programa Monitora* ICMBio and the TEAM network database have collected millions of images, where not all data has been analysed (de Oliveira Roque et al., 2018; Jansen et al., 2014; Rovero & Ahumada, 2017).

The datasets from each site resulted in 53 species in Terra do Meio, followed by 33 species in Juruena, and 20 species in Jamari. Interestingly, Jamari had the highest sampling effort. The strong differences in species richness could be related to protection status which varied between sites; whilst Terra do Meio and Juruena are strictly protected, Jamari is a sustainable-use protected area (PA) that permits the activity of reduced impact logging (RIL) (IBAMA, 2005b; Rylands & Brandon, 2005). When enforced, this form of selective logging has reduced degradation on the ecosystem, compared to other more conventional logging methods (Edwards et al., 2012; Mestre et al., 2020; Montejo-Kovacevich et al., 2018). However, the effects of RIL techniques on avian diversity, depend on the number and size of refugia left after logging (Chaves et al., 2017). Food resource availability may also be impacted by selective logging, affecting species of various feeding guilds differently (Chaves et al., 2017; Edwards et al., 2012; Gray et al., 2007; Hamer et al., 2015). In fact, Mestre et al. (2020) found that RIL in Jamari had negative effects on avian diversity, especially on dense forest specialists. These results have precedence in studies from Borneo, where RIL also disrupted

avian communities (Edwards et al., 2009; Edwards et al., 2012; Hamer et al., 2015). Moreover, roads for transporting timber from the PA interior, increase opportunities for illegal activity such as hunting and mining, increasing the overall impact (Mestre et al., 2020). Being a sustainable use PA, rather than strictly protected, may therefore have influenced the lower species richness in Jamari.

Other possible factors influencing the observed differences in species richness include PA size and surrounding degradation which also differed between sites. Terra do Meio and Juruena are both relatively large PAs, surrounded by other conservation sites (ARPA, 2011a; ICMBio, 2015; Schwartzman et al., 2013). In comparison, Jamari is smaller and does not border other PAs (IBAMA, 2005a). PA networks of considerable size offer continuous, usually undisturbed, habitat and can therefore harbour a higher species richness (Ahumada et al., 2011; Lees & Peres, 2006; Prist et al., 2012). Both, Ahumada et al. (2011) and Lees and Peres (2006) found larger forest areas and PAs to have a higher vertebrate diversity than smaller areas. In combination with this, Juruena and Jamari are located in a documented deforestation hotspot region within the Amazon (Kalamandeen et al., 2018). The forest avian community surrounding the deforestation frontier has been severely impacted, especially species relying on dense primary forest (Lees & Peres, 2006). Therefore, PA size and the regional deforestation arc probably also influenced the detected avifauna at each site.

Juruena and Jamari may have experienced more rain than Terra do Meio due to minor differences in terms of sampling effort timing. Slight variations in rainfall might have influenced avian detections, as many species move according to resource availability that is affected by seasonality (Beja et al., 2010; Costa et al., 2018; Haugaasen & Peres, 2007; Paredes et al., 2017). For example, insect abundance is higher in the dry season, as new foliage production peaks in this season (Basset et al., 2001; Haugaasen & Peres, 2005; Silva et al., 2017). On the other hand, fruit and seed resource availability is very low during the dry season (Haugaasen & Peres, 2005; Haugaasen & Peres, 2007; Hawes & Peres, 2016; Paredes et al., 2017). However, through camera trap surveys at two separate sites in the Amazon, both Mere Roncal et al. (2019) and Costa et al. (2018) did not find significant differences in terrestrial vertebrate species richness between the two seasons in unflooded forest. Therefore, there are uncertainties whether the sampling period affected the detected number of species. For future research, sampling should occur within the same period for better comparison between sites, or preferable still, throughout the entire year. Year-round sampling would uncover how avian species respond to seasonal change.

4.2. Notable findings

Knowledge on the discreet *Nothocrax urumutum* is minimal, and the camera trap detections in this study were therefore considered notable. The species is found in unflooded and seasonally flooded forests, within the Venezuelan, Colombian, Peruvian, Ecuadorian, and Brazilian Amazon (BirdLife International, 2021; Parker III, 2002; Perlo, 2009; Vizcaíno &

Rueda, 2018). Distribution maps show that Jamari lies within *N. urumutum*'s range, whilst Juruena lies just outside (BirdLife International, 2021). *N. urumutum* was previously described as solely nocturnal, due to reports from local people saying that it hides and rests during the day (Delacour & Amadon, 2004). On the other hand, local hunters have also reported diurnal feeding activity, but direct observations of this elusive bird are rare (Parker III, 2002). In the current study, only diurnal activity was detected, supporting results from other camera trap surveys (Griffiths et al., 2020; Vizcaíno & Rueda, 2018) and three direct day-time observations by Parker III (2002). *N. urumutum* sings during the night, but the location of this activity in the canopy (Delacour & Amadon, 2004; Parker III, 2002; Perlo, 2009; Vizcaíno & Rueda, 2018), i.e., outside the range of terrestrial camera trap arrays, could explain why nocturnal activity was not detected. Earlier descriptions have also considered *N. urumutum* as solitary or pair living (Vizcaíno & Rueda, 2018), but the detection of three individuals together in Juruena, along with group observations recorded in the Peruvian and Ecuadorian Amazon (Griffiths et al., 2020; Vizcaíno & Rueda, 2018), indicate a more social behaviour.

Neomorphus squamiger is another secretive species of note that was detected in this study. With few previous field observations, knowledge is severely lacking across all areas of its biology, including taxonomy, distribution, and behaviour (Firme et al., 2014; Gonçalves-Castro & Silva-Castilho, 2015). There is an ongoing debate on whether *N. squamiger* is a separate species or a sub-species of *N. geoffroyi*; the Brazilian Committee for Ornithological Records (CBRO) regards it as a separate species, whereas BirdLife International does not (BirdlLife International, 2021; de Piacentini et al., 2015; Firme et al., 2014; Gonçalves-Castro & Silva-Castilho, 2015). *N. squamiger* is endemic to the Xingu, Tapajós, Madeira, and Tocantins basins, but there are only a few distribution records for this species and its behaviour is also poorly known (Firme et al., 2014; Gonçalves-Castro & Silva-Castilho, 2015). On one occasion, this species has been observed following a flock of *Tayassu pecari* (Gonçalves-Castro & Silva-Castilho, 2015), a behaviour also observed in other *Neomorphus* spp., and probably an adaptation to utilise left-over food sources and catch insects following mammal groups (Gil et al., 2016; Gonçalves-Castro & Silva-Castilho, 2015; Haugaasen & Peres, 2013; Teixeira et al., 2014). The ten detections of *N. squamiger*, within the current study were all of solitary individuals, supporting earlier records of this species (Gonçalves-Castro & Silva-Castilho, 2015) and records of other species in the same genus (Gil et al., 2016; Teixeira et al., 2014). While no interactions between *N. squamiger* and mammals were registered, detections in this study do provide further evidence for solitary behaviour and increase the number of distribution records for this little-known species.

4.3. Species traits

Body mass had a significant positive effect on detection rate, with larger species being detected more than smaller species across all three sites. This is consistent with camera trap studies of other terrestrial vertebrates (Ahumada et al., 2013; Negroes et al., 2011; O'Brien & Kinnaird, 2008). Smaller species need to be closer to the camera lens and are therefore less

likely to be detected (Meek et al., 2012; Ortmann & Johnson, 2021; Swann et al., 2011). Ortmann and Johnson (2021) found a decrease in detection rate when species weighed less than 15 grams and when birds were more than four meters from the camera. Passive infrared sensors may also fail to detect smaller species (Meek et al., 2012; Rovero et al., 2010). The feathers on birds insulate the body heat well and may hence emit less heat (Herreid II & Kessel, 1967; Ortmann & Johnson, 2021). If the heat difference between a bird and the surrounding temperature is less than 2.7ºC or the individual is small (less surface area to emit heat) the camera trap may not be triggered (Meek et al., 2012; Rovero et al., 2013). In addition, terrestrial species usually have a greater body mass than species from higher forest strata, and since these were detected more often, this could partly explain skewed observations in relation to body size (Pearson, 1971). For this combination of reasons, camera traps are better suited to sample larger terrestrial species, and although interesting data on smaller birds can still be obtained, sample sizes tend to be lower.

Terrestrial avifauna were detected at a rate approximately three times higher than species from higher forest strata. The sampling protocol in this study targeted terrestrial vertebrates (Jansen et al., 2014; TEAM Network, 2011), and species that typically forage in higher forest strata can therefore be considered by-catch observations, even though they provide important behavioural records. Ground-based camera traps are suitable for detecting terrestrial and understorey avifauna, but inevitably only detect higher forest strata species when these might come down to the forest floor (Chmel et al., 2016; O'Brien & Kinnaird, 2008). This study was consistent with these expectations, with relatively few arboreal species detected. For a more complete inventory of species present in an area, camera traps placed at different interval heights have been found effective for sampling higher strata (Gregory et al., 2014; Moore et al., 2020), much as conducting mist-netting at midstorey and canopy levels (Chmel et al., 2016), or directly observing from cranes above or at canopy height (Walther, 2002a; Walther, 2002b). However, arboreal camera traps and canopy mist-netting are more challenging to implement as sampling techniques and thus less replicable. Therefore, sampling techniques such as spot-mapping, audio-recordings, and mist-netting, as done by Terborgh et al. (1990), in combination with ground-based camera traps, are likely to continue to provide the best coverage of species present.

The forest avian species detected filled 16 different foraging guilds, with ground-dwelling frugivores having the highest detection rates across all sites. Food resource availability could have affected the high detection rates of terrestrial frugivores. As with other food sources, the fruit availability varies both spatially and seasonally (Costa et al., 2018; Haugaasen & Peres, 2007; Hawes & Peres, 2014; Paredes et al., 2017). In terra firme forest, fruiting starts at the onset of the wet season, and fruit-falls on the forest floor reach a maximum later in this season (Costa et al., 2018; Haugaasen & Peres, 2005; Haugaasen & Peres, 2007; Hawes & Peres, 2016; Mere Roncal et al., 2019). In comparison, fruit abundance is low during the dry season (Haugaasen & Peres, 2005; Hawes & Peres, 2016; Paredes et al., 2017). During

this season, figs, which are found throughout the year, are a vital food source for frugivores (Diaz-Martin et al., 2014; Shanahan et al., 2001). *Ficus* spp. trees are unsynchronised in fruit production, and figs are therefore a patchy food source (Shanahan et al., 2001). Since sampling occurred in the dry season and transition phase to wet season, it is likely that fruit resources on the ground were low, and terrestrial frugivores were relying on the spatially distributed figs. Species from this guild may therefore have needed to search longer for food, increasing their activity and probability of being detected on camera in this period of the year.

Fourteen terrestrial insectivores were detected in Terra do Meio, and this guild was therefore the most species rich at this site. On the other hand, in Juruena and Jamari, only two and one terrestrial insectivorous species were detected, respectively. Being located within the deforestation arc of southern Amazonia, Juruena and Jamari have become drier (Costa & Pires, 2010; Negroes et al., 2011; Werth & Avissar, 2002). Apart from a regional change in climate conditions, selectively logged forests receive more light and the microclimate on the forest floor gets drier (Patten & Smith-Patten, 2012). Therefore, arthropods dependent on moist ground habitat diminish, causing cascading effects on avian insectivore specialists (Gray et al., 2007; Hamer et al., 2015; Lees & Peres, 2008; Newbold et al., 2013). In fact, terrestrial insectivores dependent on dense humid primary forest were found to be the most severely impacted avifauna group by the deforestation arc (Lees & Peres, 2008). Studies on the effects of RIL on the avifauna in Borneo also found declines in terrestrial insectivores, especially leaf-litter gleaners, after logging (Cleary et al., 2007; Edwards et al., 2009; Hamer et al., 2015). The use of RIL techniques in Jamari, together with the drier conditions caused by the deforestation arc, are likely contributing factors to the low numbers of terrestrial insectivores recorded in Juruena and Jamari.

4.4. Diel activity patterns

The general activity trend detected across all species was of heightened activity in early morning (approx. 06:00 – 08:30) and late afternoon (approx. 17:00 – 18:30). This bimodal diurnal activity pattern coincides with results from other studies in tropical regions (Mere Roncal et al., 2019; Murphy et al., 2018; Negroes et al., 2011; Pérez-Irineo & Santos-Moreno, 2017), and is commonly observed in avifauna worldwide (Robbins, 1981). Birds may avoid the hotter mid-day period and concentrate activity in the cooler mornings and evenings (Pérez-Irineo & Santos-Moreno, 2017; Pérez-Irineo & Santos-Moreno, 2021). The morning and evening air humidity levels are also often higher, increasing insect abundance, which birds may utilise for better foraging efficiency (Pérez-Granados & Schuchmann, 2020). However, although the general trend showed a bimodal diurnal activity, deviations within studied functional groups were observed.

Within the most common families (Tinamidae, Psophiidae, Cracidae and Columbidae), bimodal diurnal activity was not always prominent. Except for *Penelope* spp. and *Pipile cujubi*, all species recorded from these families were ground-dwelling (Wilman et al., 2014). The activity patterns observed among tinamids in this study support reports of strict diurnal activity

with increased activity in the morning and evening (Estevo et al., 2017; Kuhnen et al., 2013), although certain species in this family are more crepuscular or nocturnal (Brennan, 2004). The Psophiidae were more constantly active throughout the day with less distinct activity peaks, also supporting earlier research (Griffiths et al., 2020; Mere Roncal et al., 2019). Cracids are mostly active in the early morning, with a minor activity peak before sunset (Pérez-Irineo & Santos-Moreno, 2017; Pérez-Irineo & Santos-Moreno, 2021; Srbek-Araujo et al., 2012), as observed in Terra do Meio. The evening activity peaks might indicate movement to roosts, since cracids roost in higher strata (Delacour & Amadon, 2004; Srbek-Araujo et al., 2012). Columbidae were distinctly more active at sunrise and sunset in Jamari, in support of previous findings (Pérez-Granados & Schuchmann, 2020; Robbins, 1981). In Juruena on the other hand, activity was skewed towards noon. This diversion from the bimodal diurnal activity pattern may be explained by the high number of records for *Leptotila rufaxilla* during the midday period at this site. Similar observations have been reported for the activity of *L. verreauxi* in Central America (Skutch, 1964). However, in Terra do Meio *L. rufaxilla* detections were also high, but the midday activity peak was less pronounced.

Arboreal and foraging strata generalists also deviated from the bimodal diurnal activity generally observed in terrestrial species. Species from higher vertical strata were detected more towards mid-day, coinciding with observations done through point- and line-transects in earlier research (Pearson, 1971; Walther, 2002b). Similar to the observed trend of terrestrial species reducing their activity levels during the hottest periods of the day (Pérez-Irineo & Santos-Moreno, 2017; Pérez-Irineo & Santos-Moreno, 2021), arboreal species may escape the intense sunlight and highest temperatures by moving into the understorey (Pearson, 1971; Walther, 2002b). Pearson (1971) also argues that arboreal birds might follow the movement of insects down to lower strata, or that insects at higher strata have gained more energy from the heat and are therefore more difficult to catch than the less active insects in the more shaded understorey.

Although activity patterns generally had a high coefficient of overlap between sites, some significant differences were still detected. For example, Juruena and Jamari had little night-time activity, whereas in Terra do Meio avian detections occurred throughout the night. Malfunctioning of traps during the night can be ruled out, as mammals were detected throughout the night in both Juruena and Jamari. The species detected at night were, for the most part, also detected at the two other sites. Species composition is therefore unlikely the underlying reason. Except for the Common Pauraque (*Nytidromus albicollis*), which is a nocturnal species, all other species detected were mainly diurnal (Wilman et al., 2014). Few night-time detections would therefore be expected, so this is a rather unexpected result for which the underlying reasons remain unclear. Another difference between sites was the less prominent bimodal diurnal activity in Juruena, and that the first activity peak in the morning was later here than at the two other sites. Most species adapt their activity to biotic and abiotic factors in their surroundings, for instance intra- and interspecific competition, predation risk, food availability, and weather conditions (Frey et al., 2017; Halle, 2000; Mere Roncal et al.,

2019; Rowcliffe et al., 2014). Variations in activity between sites could be driven by differences in such factors (Frey et al., 2017). Investigating these environmental stimuli in more detail could shed more light on the temporal behaviour of species, but for now, the reasons for these activity differences remain speculative.

5. Conclusion

To the best of my knowledge this is the first study to include and attempt to identify all avian species captured on wildlife cameras from camera trap surveys performed in the Amazon. From the 4,134 independent detections recorded, 87.4% were identified to species level, which resulted in a total of 66 species from 51 genera, 31 families, and 16 different orders.

The camera trap effort yielded a relatively high avian species richness, with strong differences between the three sites investigated. These differences, particularly within terrestrial insectivores, appears to suggest that surrounding deforestation may have consequences even for the avifauna within intact nearby forests. The RIL techniques used in Jamari, and the deforestation arc of southern Amazonia, likely caused drier climate conditions in Juruena and Jamari, probably impacting food resource availability and thus also affecting avifauna. This study also contributes to support earlier findings of diurnal and gregarious behaviour in *Nothocrax urumutum* and solitary behaviour in *Neomorphus squamiger*. The detections of these two little-known species shows the high value of remote cameras in acquiring more knowledge on terrestrial elusive species. Large ground-dwelling species were most frequently observed at all three sites and underlines that the use of wildlife cameras is most adequate for monitoring terrestrial vertebrates of larger body size. The activity patterns observed indicate a response to heat stress; terrestrial species were observed to be most active in the cooler mornings and evenings, and arboreal species escaped to lower strata during mid-day. Variations, although minor, in activity patterns were observed between sites, showing a need for future research on how environmental factors influence diel activity patterns in avian communities.

Through these findings, I demonstrated the usefulness of camera traps as a tool for biodiversity surveys. The non-invasive nature of camera traps and ability to be left autonomously in the field for several weeks allows for the collection of large amounts of data that would otherwise be much more challenging. Studies analysing such extensive datasets usually ignore certain camera trap footage, therefore there are large amounts of untapped data already collected but so far not analysed. This study shows that avifaunal records from existing camera trap data can be reliably identified and yield important findings. Although the current study demonstrates the value of including all avifaunal detections, it also provides evidence that ground-based camera trapping alone is not sufficient for a complete community-wide perspective. For even better coverage, camera traps are recommended to be used in combination with other sampling methods, such as spot-mapping, audio-records, and mist-netting.

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Appendix 1: Map over sampling area in Terra do Meio Ecological Station
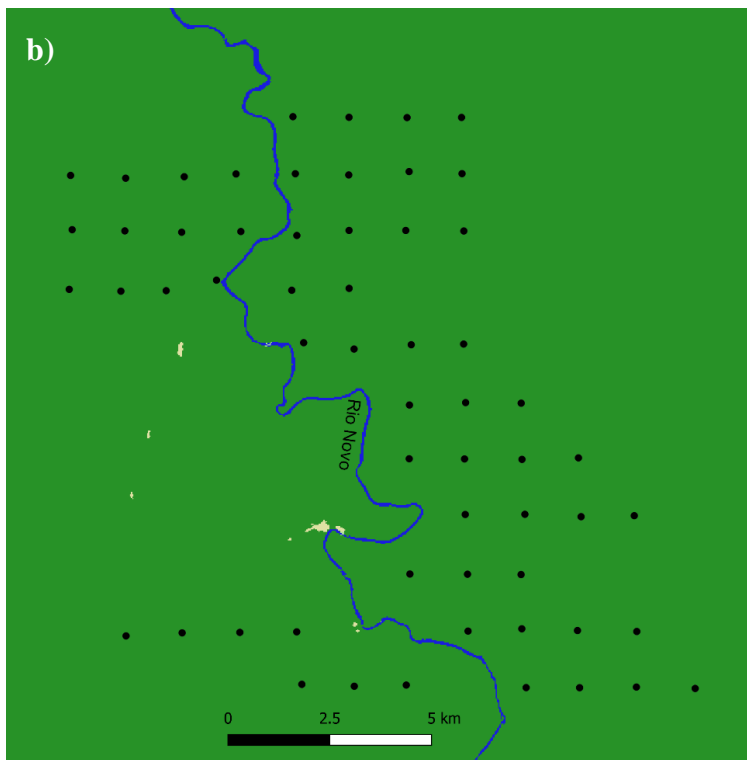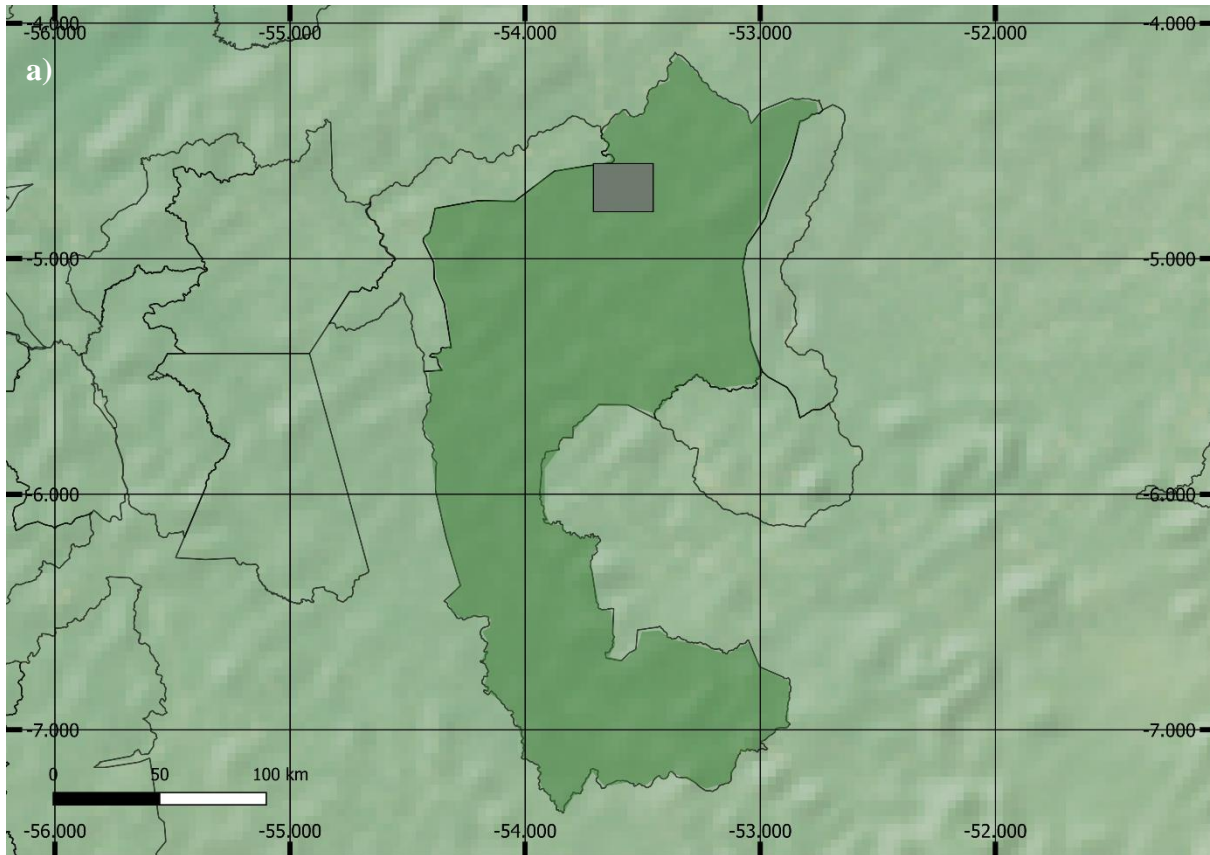
Figure A1: Map over Terra do Meio Ecological Station (a) represented by darker shaded green, with survey site shown with dark grey area. Black bordered areas represent surrounding protected areas. Camera trap array (b; each black dot is a camera trap site) placed in the Novo river basin with one trap placed per 2 km^2.

Background raster downloaded from Natural Earth (a) (www.naturalearthdata.com; Natural Earth, 2009-2021) and MAPBIOMAS v.5.0 (b) (mapbiomas.org; MapBiomas Project, 2019)

Appendix 2: Map over the sampling area in Juruena National Park
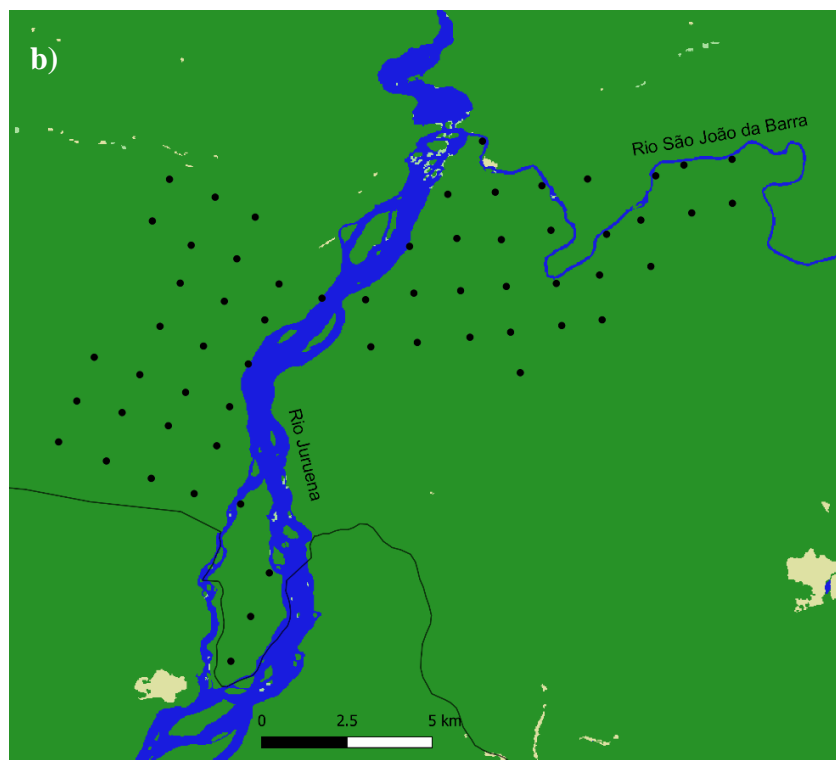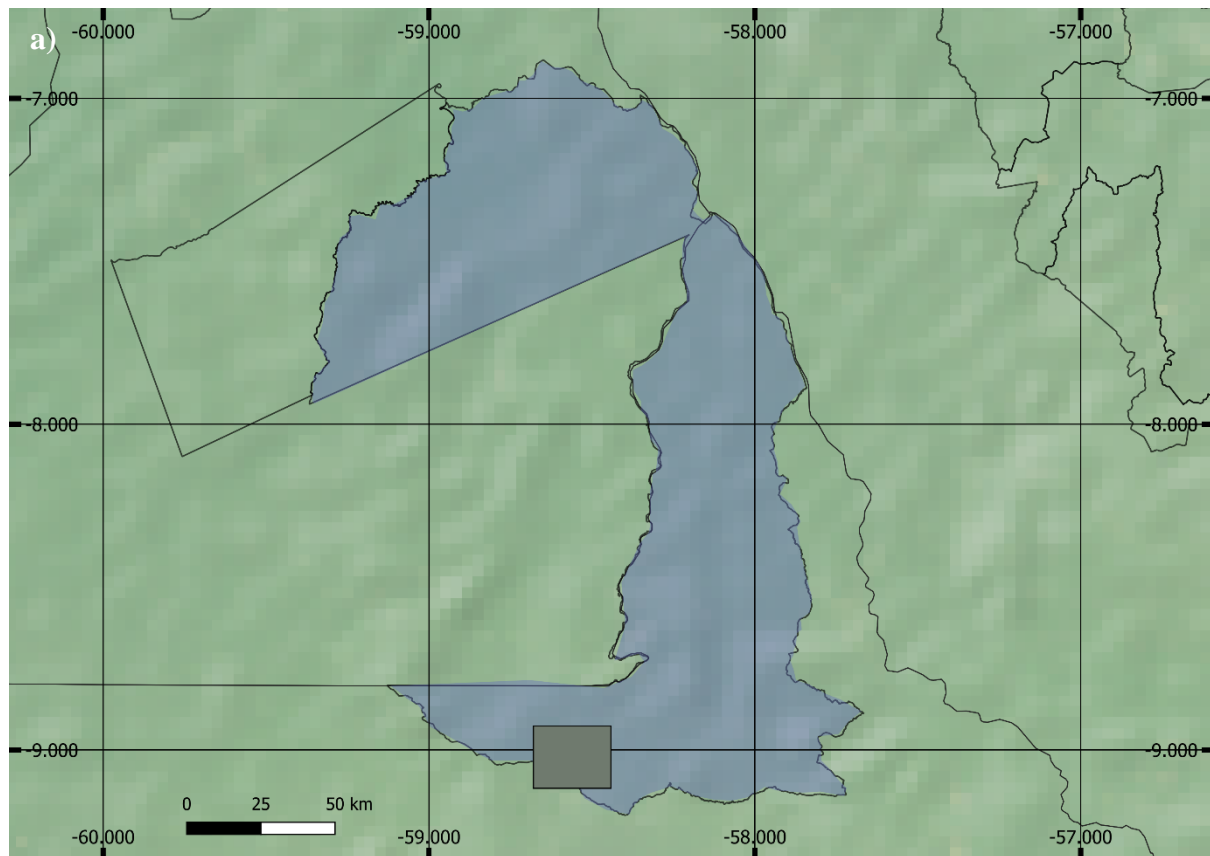
Figure A2: *Map over Juruena National Park (a) shaded in blue, with survey site shown with dark grey area. Black bordered areas represent surrounding protected areas. Camera trap array (b; each black dot is a camera trap site) placed in the Juruena and São de João da Barra river basins with one trap placed per 2 km².*

Background raster downloaded from Natural Earth (a) (www.naturalearthdata.com; Natural Earth, 2009-2021) and MAPBIOMAS v.5.0 (b) (mapbiomas.org; MapBiomas Project, 2019)

Appendix 3: Map over the sampling area in Jamari National Forest
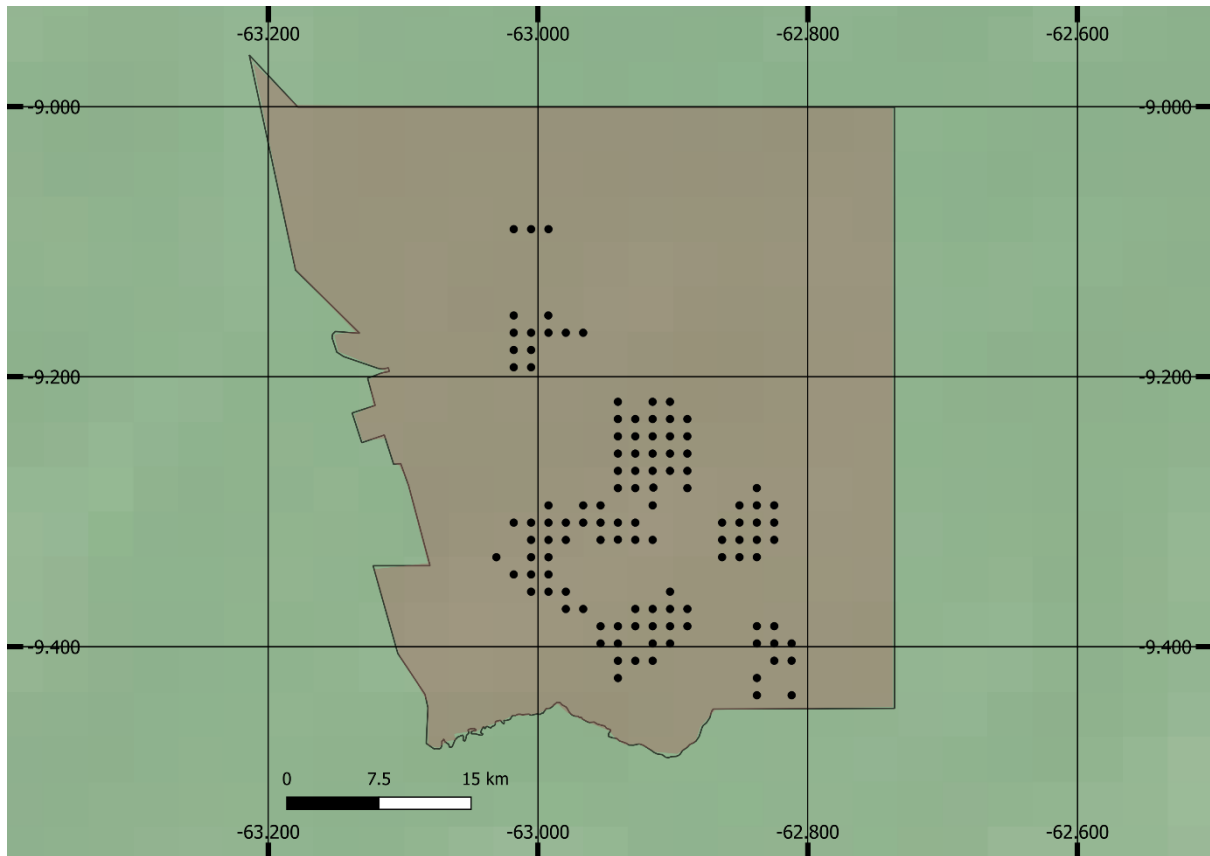
Figure A3*: Map over Jamari National Forest shaded in red, with camera trap arrays (each black dot is a camera trap site) placed with one trap per 2 km².*

Background raster downloaded from Natural Earth (www.naturalearthdata.com; Natural Earth, 2009-2021)

Appendix 4: Species list

Table A1: *List of the detected species including their taxonomy following the Brazilian Ornithological Records Committee (de Piacentini et al., 2015) and common names. "Unknown" is used when the specific taxonomical level was not identified. The number of independent detections and photos (in parenthesis) per site (TDM: Terra do Meio; PNJ: Juruena; JAM: Jamari), number of independent detections within each diel period (day, night, and twilight), and characterising traits are listed for each species. The traits section is divided into body mass (Mass; in grams), size (s: small; ≤100g, m: medium; >100g & ≤600g, L: large; >600g), foraging guild (Guild; diet: Gr - Granivore (seed-eater), Fr - Frugivore (fruit-eater), In - Insectivore (insect-eater), Pr - Predator (predating on all vertebrates except for fish), Sc - Scavenger (feeding on carcases), Om - Omnivore (when the other categories were not dominant, less than 50%, or 50%:50% plant and animal matter, and foraging stratum: Aquat. - Aquatic, T - Terrestrial, TU - Terrestrial/Understory, U - Understory, A - Arboreal, TUA - Terrestrial/Understory/Arboreal (forest strata generalist)) and whether these are based on species (Spp.) or genus (Gen.) average (EltonTraits; Wilman et al., 2014; Terborgh et al., 1990).*

| Species | | Common Name | No. detections (No. photos) | | | Diel period[1] | | | Traits | | | |
			TDM	PNJ	JAM	Day	Night	Twilight	Mass (g)	Size	Guild	Based on
TINAMIFORMES												
TINAMIDAE												
Tinamus	*tao*	Gray Tinamou	102 (1024)	34 (339)	42 (270)	171	1	6	1600	L	T Om	Spp.
	major	Great Tinamou	201 (1989)	33 (326)	23 (135)	249	-	8	1026	L	T Om	Spp.
	guttatus	White-throated Tinamou	10 (129)	1 (3)	26 (159)	37	-	-	686	L	T Fr	Spp.
	spp.	-	27 (131)	19 (113)	10 (54)	53	1	2	916	L	T Om	Gen.
Crypturellus	*cinereus*	Cinereous Tinamou	36 (402)	11 (66)	9 (63)	51	4	1	507	M	T Fr	Spp.
	undulatus	Undulated Tinamou	16 (99)	5 (33)	6 (31)	25	-	2	564	M	T Fr	Spp.
	variegatus	Variegated Tinamou	98 (781)	5 (42)	17 (87)	115	-	5	378	M	T Fr	Spp.
	soui	Little Tinamou	8 (48)	-	1 (6)	9	-	-	216	M	T Om	Spp.
	strigulosus	Brazilian Tinamou	102 (1340)	1 (3)	-	91	9	3	431	M	T Om	Spp./Gen.
	obsoletus	Brown Tinamou	-	1 (3)	-	1	-	-	443	M	T Om	Spp.
	spp.	-	26 (134)	3 (27)	3 (18)	29	1	3	399	M	T Om	Gen.
unknown		-	6 (18)	5 (19)	12 (42)	20	-	3	-	-	-	-

Species		Common Name	No. detections (No. photos)			Diel period[1]			Mass (g)	Size	Traits	Based on
			TDM	PNJ	JAM	Day	Night	Twilight			Guild	
GALLIFORMES												
CRACIDAE												
Penelope	*pileata*	White-crested Guan	29 (544)	-	-	28	-	1	1250	L	A Fr	Spp./Gen.
	superciliaris	Rusty-margined Guan	83 (1196)	2 (15)	6 (45)	84	2	5	895	L	A Fr	Spp.
	jacquacu	White-browed Guan	-	18 (150)	20 (167)	38	-	-	1488	L	A Fr	Spp.
	spp.	-	6 (24)	-	1 (3)	7	-	-	1283	L	A Fr	Gen.
Pipile	*cujubi*	Red-throated Piping-Guan	-	1 (6)	-	1	-	-	1196	L	A Fr	Spp./Gen.
Nothocrax	*urumutum*	Nocturnal Curassow	-	1 (129)	3 (36)	4	-	-	1700	L	T Fr	Spp./Gen.
Mitu	*tuberosum*	Razor-billed Curassow	307 (7733)	236(8574)	208 (2886)	740	5	6	2769	L	T Fr	Spp.
Crax	*fasciolata*	Bare-faced Curassow	107 (2871)	18 (186)	-	118	-	6	2600	L	T Fr	Spp.
ODONTOPHORIDAE												
Odontophorus	*gujanensis*	Marbled Wood-Quail	79 (974)	-	-	78	-	1	314	M	T Om	Spp.
	stellatus	Starred Wood-Quail	-	-	3 (12)	3	-	-	336	M	T Om	Spp./Gen.
PELECANIFORMES												
ARDEIDAE												
Pilherodius	*pileatus*	Capped Heron	-	-	1 (9)	1	-	-	569	M	Aquat.	Spp.
Tigrisoma	*lineatum*	Rufescent Tiger-Heron	2 (6)	6 (45)	-	7	-	1	813	L	Aquat.	Spp.
THRESKIORNITHIDAE												
Mesembrinibis	*cayennensis*	Green Ibis	9 (66)	1 (6)	-	9	-	1	756	L	Aquat.	Spp.

			No. detections (No. photos)			Diel period[1]					Traits	
Species		Common Name	TDM	PNJ	JAM	Day	Night	Twilight	Mass (g)	Size	Guild	Based on
CATHARTIFORMES												
CATHARTIDAE												
Cathartes	*melambrotus*	Greater Yellow-headed Vulture	2 (15)	1 (24)	-	3	-	-	1373	L	T Sc	Spp.
ACCIPITRIFORMES												
ACCIPITRIDAE												
Buteo	*nitidus*	Gray-lined Hawk	-	1 (6)	-	1	-	-	519	M	A Pr	Spp.
Buteogallus	*urubitinga*	Greater Black Hawk	-	1 (9)	3 (54)	4	-	-	1153	L	A Pr	Spp.
EURYPYGIFORMES												
EURYPYGIDAE												
Eurypyga	*helias*	Sunbittern	12 (123)	-	-	11	-	1	210	M	Aquat.	Spp.
GRUIFORMES												
PSOPHIIDAE												
Psophia	*viridis*	Green-winged Trumpeter	-	78 (1035)	127 (1172)	199	-	6	1071	L	T Fr	Spp.
	dextralis	Brown-winged Trumpeter	393 (5596)	43 (558)	-	417	3	16	1138	L	T Fr	Gen.
RALLIDAE												
Aramides	*cajanea*	Gray-necked Wood-Rail	25 (342)	6 (39)	-	31	-	-	397	M	Aquat.	Spp.
COLUMBIFORMES												
COLUMBIDAE												
Geotrygon	*montana*	Ruddy Quail-Dove	50 (409)	43 (293)	104 (546)	186	1	10	134	M	T Gr	Spp.
Leptotila	*rufaxilla*	Gray-fronted Dove	209 (1498)	98 (1251)	-	306	-	1	157	M	T Gr	Spp.
	verreauxi	White-tipped Dove	9 (45)	5 (54)	-	14	-	-	147	M	T Gr	Spp.
	spp.	-	49 (194)	15 (75)	2 (9)	63	-	3	165	M	T Gr	Gen.
unknown		-	297 (3379)	-	3 (12)	223	67	10	-	-	-	-

Species		Common Name	No. detections (No. photos)			Diel period[1]			Mass (g)	Size	Traits Guild	Based on
			TDM	PNJ	JAM	Day	Night	Twilight				
CUCULIFORMES												
CUCULIDAE												
Neomorphus	*squamiger*	Scaled Ground-Cuckoo	10 (60)	-	-	10	-	-	355	M	T In	Spp.
STRIGIFORMES												
STRIGIDAE												
Glaucidium	*brasilianum*	Ferruginous Pygmy-Owl	1 (3)	-	-	-	1	-	75	S	T Pr	Spp.
Megascops	spp.	-	-	1 (3)	-	1	-	-	134	M	TUA Pr	Gen.
CAPRIMULGIFORMES												
CAPRIMULGIDAE												
Nyctidromus	*albicollis*	Common Pauraque	7 (27)	2 (6)	-	2	-	7	58	S	TUA In	Spp.
unknown		-	-	2 (10)	-	1	-	1	-	-	-	-
CORACIIFORMES												
MOMOTIDAE												
Momotus	*momota*	Amazonian Motmot	22 (101)	1 (3)	-	19	1	3	115	M	TUA In	Spp.
GALBULIFORMES												
BUCCONIDAE												
Monasa	*morphoeus*	White-fronted Nunbird	62 (477)	-	-	62	-	-	88	S	TUA In	Spp.
	nigrifrons	Black-fronted Nunbird	3 (12)	1 (6)	-	4	-	-	81	S	TUA In	Spp.
	spp.	-	-	1 (1)	-	1	-	-	81	S	TUA In	Gen.
PICIFORMES												
PICIDAE												
Campephilus	*rubricollis*	Red-necked Woodpecker	3 (18)	-	-	3	-	-	211	M	A In	Spp.
Celeus	*elegans*	Chestnut Woodpecker	-	1 (3)	-	1	-	-	135	M	A In	Spp./Gen.

			No. detections (No. photos)			Diel period[1]					Traits	
Species		Common Name	TDM	PNJ	JAM	Day	Night	Twilight	Mass (g)	Size	Guild	Based on
FALCONIFORMES												
FALCONIDAE												
Micrastur	*mintoni*	Cryptic Forest-Falcon	1 (3)	-	1 (3)	2	-	-	210	M	U Pr	Spp.
PASSERIFORMES												
THAMNOPHILIDAE												
Taraba	*major*	Great Antshrike	1 (3)	-	-	1	-	-	59	S	TUA In	Spp.
Myrmoborus	*myotherinus*	Black-faced Antbird	8 (20)	-	1 (3)	8	-	1	19	S	TU In	Spp.
Hylophylax	*punctulatus*	Dot-backed Antbird	1 (3)	-	-	1	-	-	12	S	TUA In	Spp.
Phlegopsis	*nigromaculata*	Black-spotted Bare-eye	1 (9)	-	-	1	-	-	45	S	T In	Spp.
Myrmornis	*torquata*	Wing-banded Antbird	2 (12)	-	-	1	-	1	47	S	T In	Spp.
Myrmelastes	*rufifacies*	Rufous-faced Antbird	1 (6)	-	-	1	-	-	26	S	T In	Spp.
Rhegmatorhina	*gymnops*	Bare-eyed Antbird	3 (36)	-	-	3	-	-	29	S	T In	Spp.
CONOPOPHAGIDAE												
Conopophaga	*aurita*	Chestnut-belted Gnateater	1 (3)	-	-	1	-	-	26	S	T In	Spp.
GRALLARIIDAE												
Grallaria	*varia*	Variegated Antpitta	18 (118)	-	-	13	-	5	119	M	T In	Spp.
Hylopezus	*berlepschi*	Thrush-like Antpitta	13 (52)	1 (3)	-	1	-	-	47	S	T In	Spp.
Myrmothera	*campanisona*	Amazonian Antpitta	-	-	1 (3)	12	-	2	48	S	T In	Spp.

			No. detections (No. photos)			Diel period[1]			Traits			
Species		Common Name	TDM	PNJ	JAM	Day	Night	Twilight	Mass (g)	Size	Guild	Based on
FORMICARIIDAE												
Formicarius	*analis*	Black-faced Antthrush	40 (145)	-	-	40	-	-	62	S	T In	Spp.
	colma	Rufous-capped Antthrush	70 (396)	1 (3)	-	65	-	6	47	S	T In	Spp.
	spp.	-		1 (3)	-	1	-	-	60	S	T In	Gen.
Chamaeza	*nobilis*	Striated Antthrush	136 (1265)	-	-	61	3	72	123	M	T In	Spp./Gen.
DENDROCOLAPTIDAE												
Dendrocolaptes	*ridgwayi*	Ridgway's Woodcreeper	1 (3)	-	-	1	-	-	69	S	A In	Spp.
unknown	spp.	-		1 (2)	-	1			-	-	-	-
FURNARIIDAE												
Sclerurus	*rufigularis*	Short-billed Leaftosser	1 (9)	-	-	1	-	-	22	S	T In	Spp.
TITYRIDAE												
Schiffornis	*turdina*	Thrush-like Schiffornis	13 (93)	1 (3)	-	11	1	2	32	S	U Om	Spp.
TURDIDAE												
Turdus	*fumigatus*	White-necked Thrush	5 (16)	-	-	5	-	-	54	S	T In	Spp.
	albicollis	Cocoa Thrush	26 (95)	-	-	25	-	1	76	S	TU Om	Spp.
	spp.	-	12 (40)	1 (3)	-	7	-	5	76	S	T Om	Gen.
unknown		-		1 (2)	-	1	-	-	-	-	-	-
PASSERELLIDAE												
Arremon	*taciturnus*	Pectoral Sparrow	8 (34)	-	-	8	-	-	25	S	TU Om	Spp./Gen.
PARULIDAE												
Myiothlypis	*mesoleuca*	Riverside warbler	2 (9)	-	-	2	-	-	14	S	T In	Spp.

Species		Common Name	No. detections (No. photos)			Diel period[1]			Mass (g)	Size	Traits Guild	Based on
			TDM	PNJ	JAM	Day	Night	Twilight				
ICTERIDAE												
Cacicus	*solitarius*	Solitary Black Cacique	-	1 (9)	-	1	-	-	80	S	A In	Spp.
Psarocolius	*decumanus*	Crested Oropendola	-	-	1 (3)	1	-	-	206	M	A Om	Spp.
THRAUPIDAE												
Saltator	*grossus*	Slate-colored Grosbeak	1 (3)	-	-	1	-	-	44	S	A In	Spp./Gen.
CARDINALIDAE												
Cyanoloxia	*rothschildii*	Rothschild's Blue Grosbeak	1 (3)	-	-	1	-	-	33	S	T Fr	Spp.
Habia	*rubra*	Scarlet-throated Ant-Tanager	1 (3)	-	-	1	-	-	38	S	A In	Gen.
FAMILY UNKNOWN												
unknown		-	8 (21)	-	-	6	-	2	-	-	-	-
ORDER UNKNOWN												
FAMILY UNKNOWN												
unknown		-	4 (11)	-	3 (7)	7	-	-	-	-	-	-
Totals												
Species:		66	53	33	20							
No. detections:		4,134	2,793	703	638	3,824	100	210				
No. photos:		53,646	34,237	13,471	5,838							

[1] Diel period: day between sunrise (06:22) and sunset (18:26), night from the end of nautical dusk till the nautical dawn, and twilight from the start of nautical dawn till sunrise and from sunset till end of nautical dusk.

X