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Population density estimation of meso-mammal carnivores using camera traps without the individual recognition in Maduru Oya National Park, Sri Lanka

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Abstract

Reliable population estimates are crucial for the conservation and management of faunal species. Population data of meso-mammal carnivores in Sri Lanka, as well as elsewhere in the world, is scarce. We estimated population densities of meso-mammal carnivores in Maduru Oya National Park (MONP) using Random Encounter Model (REM) and Camera Trap Distance Sampling (CTDS) methods in this study. A total of 3,402 camera trapping days yielded 3,357 video captures of 69 different animal taxa including 658 video captures of meso-mammal carnivores. In this study, we recorded all 12 meso-mammal carnivore species found on the island. The two density estimate methods generated similar population estimates indicating that both methods are compatible to be applied in tropical forest habitats for meso-carnivore species. We identify MONP as an area with high richness for the focal species. The study also generated movement speed, activity patterns, activity levels, and day ranges for the focal species, which will be useful for future research. We discuss the population density estimates for different meso-carnivore species and the use of REM and CTDS density estimation methods and their applicability to a tropical meso-carnivore community.

Keywords: *Random Encounter Model, Camera Trap Distance Sampling, population monitoring, activity level, day range, species abundance*

Introduction

Accurate and updated population density estimates are vital for the proper evaluation of the conservation status of species, as well as for the management and decision-making about wildlife populations (Luo et al. 2020; Romairone et al. 2018; Jiménez et al. 2017; Royle et al. 2013; Carbone et al. 2006). Focused research on estimating mammalian carnivore populations remains scarce in Sri Lanka. Although there have been efforts on estimation of the population density of the Sri Lankan leopard (*Panthera pardus kotiya*) – the apex predator of the country (Webb et al. 2020; Kittle and Watson 2018; Kittle et al. 2017) – the population densities of many other species of mammalian carnivores have not been assessed (Kittle and Watson 2018; Miththapala 2018; Wijesinghe 2006; Weerakoon and Goonatilake 2006). In this study, we focused our work on estimating the population densities of meso-mammals of the order Carnivora (meso-carnivores/small carnivores) that inhabit Maduru Oya National Park in the dry zone of Sri Lanka. Meso-mammals are defined as "medium sized mammals larger than rodents, up to roughly fox/jackal sized" (Parker at al. 2012; Hoffmann et al. 2010), "which are between 150g-10kg in weight" (Morrison 2013).

Several factors such as the difficulty of individual recognition (Johansson et al. 2020) for spatial capture recapture (SCR) density estimate models, nocturnal/elusive behaviour, solitary activity and high costs of live-trapping methods (Hardouin et al. 2021; Romairone et al. 2018; Sheftel 2018; O'Brien 2011; Rowcliffe et al. 2008; Silveira et al. 2003) have influenced the lack of information for these species. Meso-mammals of the order Carnivora include an ecologically important guild of species that plays key roles as predators, seed dispersers, as well as influencers of community structures in tropical forest ecosystems, regulating lower trophic levels and maintaining biodiversity (Hardouin et al. 2021; Kalle 2013; Kalle et al. 2013; Roemer et al. 2009). They are also considered carriers of diseases, agricultural pests and apex predators in some ecosystems (Roemer et al. 2009). This group of mammals is represented in Sri Lanka by the families Felidae (small wild cats), Herpestidae (mongooses), Viverridae (civets), Mustelidae (otter) and Canidae (jackal). Within these families, there are 12 species (Annex I) in Sri Lanka (Hunter 2019; MoMD&E 2019; Dittus 2017; Weerakoon 2012).

With advancements in camera trapping technology, there has been a rise in research based on camera trapping methods (Green et al. 2020; Meek et al. 2020; Glover-Kapfer et al. 2019; Meek et al. 2014; O'Brien 2011). The scope of these studies spreads across a wide range of different ecological facets such as faunal checklists, abundance, density estimations, population monitoring, behavioural studies, species specific focal research studies and wildlife management (Cappelle et al. 2021, Rovero et al. 2013; Meek et al. 2012; Bater et al. 2011; Zimmermann et al. 2011; O'Brien 2011; TEAM Network 2011; Clevenger et al. 2009; Tobler et al. 2009; Bowkett et al. 2008; Rovero and De Luca 2007; Karanth et al. 2006; Sanderson and Trolle 2005). However, there remained the absence of a reliable and cost-effective method of population density estimation of mammalian fauna that cannot be recognised individually (Chatterjee et al. 2020; Gilbert et al. 2020; Rowcliffe et al. 2008; Srbek-Araujo and Chiarello 2005). This lacuna was filled by the Random Encounter Model (REM) developed by Rowcliffe et al. (2008) after the early efforts of occupancy-based models (Royle and Nichols 2003) and *N*-mixture models (Royle 2004) for abundance estimation. Since then, there has been several research studies that have been conducted based on REM model (Palencia et al. 2021b; Pfeffer et al. 2017; Rademaker et al. 2016; Manzo et al. 2012) as well as modified methods such as the Random Encounter and Staying

Time (REST) by Nakashima et al. (2017). Spatial count (SC) models (Chandler and Royle 2013), time-lapse based models (Moeller et al. 2018), spatial presence-absence (SPA) models (Chatterjee et al. 2020; Ramsey 2015) and species space use (SPU) models (Luo et al. 2020) for populations without markings are several other methods that were recently developed each with their own or common limitations. With the rapid technological development of digital camera traps, the video recording capability of camera traps and multiple snapshots with faster trigger speeds have paved the way for development of REST model (Nakashima et al. 2017) and recently, the modified camera trap distance sampling (CTDS) method (Howe et al. 2017) of the well-known 'Distance Sampling' (DS) approach (Thomas et al. 2010; Buckland et al. 2015, 2004, 2001).

Instead of using the auxiliary data such as day range determined by telemetry methods to support the REM, during the last decade, this method has evolved to be self-supplemented based solely on camera trapping information (Hofmeester et al. 2017; Rowcliffe et al. 2016, 2011, 2008). The process of calculating the species densities using REM generates several important parameters such as animal speed, activity level and day range, which then supports a variety of ecological studies. Therefore, REM has provided a means to investigate a wider range of ecological parameters to assist in the species conservation and management.

After the modifications of Howe et al. (2017), the DS method – which has been well established over the years – can also be used to determine species densities even when individual markings are absent. Distance sampling can be considered one of the most applied methods for monitoring of wildlife populations (Buckland et al. 2015; Buckland et al. 2001; Thomas et al. 2010). However, the traditional DS method was more applicable for species that could be detected easily and directly during the surveys (Corlatti et al. 2020; Buckland et al. 2015). When it comes to rare, elusive and smaller animal species, the applicability was low (Corlatti et al. 2020; Marques et al. 2013). As a result, in the recent past, there has been a rise in usage of passive DS methods such as sonar, radar and acoustic surveys (Corlatti et al. 2020; Buckland et al. 2015; Marques et al. 2013). The implementation of CTDS (another passive DS method) can be considered a revolution in the wildlife population monitoring study methods, as it greatly reduces the limitations that previously prevailed. Availability of user-friendly software and R packages together with adequate methodologies and literature will make CTDS more popular in future camera trap based research work. Since its introduction, CTDS method has generated reliable density estimates in most of the recent studies (Cappelle et al. 2021; Palencia et al. 2021b; Bessone et al. 2020; Harris et al. 2020; Cappelle et al. 2019).

In this study, the SCR methods where individual recognition is required were not selected, because there were no identifiable pelage patterns in most of the focal species except for the Felids. Therefore, as the best alternatives, we selected REM and CTDS methods of density estimation using camera traps. Most of the recent REM and CTDS camera trapping applications have focused on larger ungulate species (Pal et al. 2021; Pfeffer et al. 2017; Rovero and Marshall 2009) or on single species (Corlatti et al. 2020; Harris et al. 2020; Cappelle et al. 2019; Gray 2018; Cusack et al. 2015; Anile et al. 2014; Engeman et al. 2013; Manzo et al. 2012). Rich et al. (2019) investigated population density of multiple forest carnivore species, using SCR methods. The number of camera trap studies on population densities of meso-mammal carnivores remains low and CTDS based multi-species evaluations of this group of fauna are limited (Cappelle et al. 2021; Palencia et al. 2021b; Hardouin et al. 2021; Bessone et al. 2020). Therefore, this is one of the early applications of these new methods to a tropical meso-carnivore community and the first multi-species density estimation in Sri Lanka.

The objectives of this study were; i) to generate density estimates for the meso-mammal carnivores in MONP; ii) to compare the density estimates derived from REM and CTDS methods and assess their applicability in practical situations. During the process of generating density estimates, we developed activity levels, activity patterns, day range, and detection radius/distance parameters for the focal species. Hence, the results generated through this study will provide a range of information to fill research gaps and to benefit future conservation and management requirements.

Materials and Methods

Study area

We conducted this study in Maduru Oya National Park (588 km^2) situated in the dry zone (predominantly, in the northern and eastern parts of the country) (Punyawardena 2020) of Sri Lanka. We carried out camera trapping in the western flank of the park adjacent to the western bank of the Maduru Oya reservoir situated in the centre of the park (Fig. 1). The area of study was 304km^2 – comprising grasslands, shrublands and the climax habitat of dry mixed evergreen forest. Rocky outcrops can be observed in patches scattered throughout the park

(Jayasekara et al. 2021). Most of the grasslands and shrublands are a result of slash and burn cultivation practised over the years, until the area was declared a national park in 1983 (IUCN 1990). The grasslands assume characteristics of savannas in some areas, whereas the reservoir perimeter is surrounded by seasonal grasses that grow during the dry season (late January-October). The park is well known for large numbers of sightings of Asian elephants (*Elephas maximus*) and also provides habitats for many other mammalian species (Jayasekara and Mahaulpatha 2019) as well as avifauna (Dissanayake 1995). The large Maduru Oya reservoir (6,100ha), constructed as a part of the Mahaweli Development Project (a large-scale national irrigation project to harness water from Sri Lanka's largest river – the Mahaweli), situated at the centre of the park, has a considerable influence on this faunal assemblage and creates a large perimeter (97.8 km) with aquatic, riparian habitats. We selected the western flank of the park for our study because the natural barriers and the man-made reservoirs/canals help in fulfilling one key assumption of both REM and CTDS models – the requirement of a closed population (Howe et al. 2017; Rowcliffe et al. 2008). Most of the study area is surrounded by four large reservoirs, irrigation canals, rock formations, and cultivated lands surround (Fig. 1) (IUCN 1990).

Camera trapping

We conducted camera trapping mostly during the dry season (compared to the monsoon season from October to January) (IUCN 1990) adhering to the protocol for tropical forest vertebrate camera trap survey by Team Network (2011). We divided the selected study area in to 2 X 2 km plots using a feature grid in ArcMap version 10.4.1 (Esri, Redlands, USA) (Fig. 1). Generating this grid fulfils the spacing requirement recommended by Team Network (2011) of placing one camera in every 2 km^2 grid plot. We used two infra-red-triggered camera models: Browning Strike Force HD Pro (n=10, low glow flash) and Browning Dark OPS HD Pro (n=15, no glow flash) (Browning, USA). Except for the type of flash, the specifications of the two camera models were similar. We especially used these flash types to reduce interference to animals and meet the assumption of independent animal movement (Rowcliffe et al. 2008).

We established camera trap stations in 90 plots. We excluded plots covered with large areas of reservoir, inaccessible terrain and some plots with repetitive habitats, to obtain a balanced sampling effort in all available habitat types (Rovero et al. 2013). We deployed the moving survey method (Palencia et al. 2021b) to better use the available cameras which increase the sampling effort and precision. One station had to be excluded from analyses because a camera was stolen by a poacher, reducing the total sampling points to 89. We randomly selected plots and we placed cameras within each selected plot moving in a random distance from a random starting point in the grid line of the plot gird (walking perpendicularly to the grid line). This randomisation of camera stations fulfils the requirement of both REM and CTDS methods. Usually, we attached cameras at a fixed height of 25 cm to tree trunks or an erected log. We selected this height based on previous literature (Kalle 2013) and our field experience of camera trapping meso-mammal carnivores, to maximise detection. We oriented cameras in a northward direction. We had to deviate the realised sampling locations and orientations up to a maximum of 100 m and 40° respectively to ensure cameras were mounted at suitable locations without obstructions (Pfeffer et al. 2017; Howe et al. 2017). However, we remained as close as possible to the predefined coordinates and orientation. We ensured mounting cameras parallel to the ground and to avoid areas with slopes, to obtain accurate distance measurements during analyses. We used protective metal cases and python lock cables when mounting cameras, to reduce damage from elephant attacks and theft. We set all cameras to function for 24 hrs in a stretch of 38.2 days on average. We set the range parameter to "long range", mode of capture to "video" and trigger delay to one second. These specifications ensured that capture data could be used for both the REM and CTDS methods. We monitored the camera stations on a routine basis of 10-15 days and stations with defects in cameras/memory cards were resampled to obtain the desired sampling effort. We had to reassign two camera stations where initial coordinates coincided with resting places of a fishing cat and ring-tailed civets.

Random Encounter Model

We used REM developed by Rowcliffe et al. (2008) as one method of meso-mammal carnivore density (D km^{-2}) estimation. The equation,

$$\mathrm{D} = \frac{y}{t} \times \frac{\pi}{v * r * (2 + \theta)}$$

is used for the calculation where y denotes the number of capture events; t, the survey effort (camera trapping days); v, the average daily distance travelled (km/day); r, the average distance to the first capture of animals (km); and the average angle to the capture animals is θ (radians). The daily distance travelled (v, day range) is derived using the movement speed (s) and activity level (*a*) of animals following the equation shown below.

$$v = s \times a$$

The movement speed (s) of each animal was derived using the simple equation $s_i = \frac{d_i}{t_i}$ (Pfeffer et al. 2017) where d_i denotes the distance travelled and t_i the time duration. We followed the procedure described by Rowcliffe et al. (2016) to calculate the average speed parameter by fitting probability distributions to samples of individual speed observations obtained from video captures instead of multiple snapshots. The R package '*fitdistrplus*' (Delignette-Muller and Dutang 2015) was used for model fitting and best fitting models were selected based on Akaike Information Criterion (AIC) values.

To determine activity level (a) and the proportion of the day a species is active (Rowcliffe et al. 2016), we used the R package '*activity*' (Rowcliffe, 2019; Rowcliffe et al. 2014). We converted the time stamp data of species captured on camera trap videos to radian time and analysed this in R with 1,000 iterations.

To determine the radial distance (r) to the capture animal and d_i, accurate evaluation of distance from the camera was highly important. The method generally used for distance estimation is based on marking certain distance intervals from the camera at the time of mounting camera traps (Palencia et al. 2021b; Pfeffer et al. 2017; Caravaggi et al. 2016) or measuring distances of each animal manually at time of dismounting (Rowcliffe et al. 2011). However, we found that this method required extra time and effort in the field and that visual estimation of distances outside the marking points was difficult. In addition, in MONP where elephant activity was quite high, spending extended time in certain locations was dangerous. Therefore, we deviated from the original method of measuring distance. Rather than measuring distances on location, we incorporated the distance intervals in a pre-marked grid (Caravaggi et al. 2016) (Fig. 2), as a standard which could be superimposed on all camera trap records. This method made the determination of distances and trigonometric calculation of distances (Pfeffer et al. 2017; Caravaggi et al. 2016) easier and accurate (a distance-angle table generated following this method is given in Annex II. We calculated the time difference (t_i) from the time difference recorded in each video capture. Instead of camera specific detection distance and angles (Rowcliffe et al. 2008), for our analyses, we used species specific average detection distances (ADD); average detection angles (θ, ADA) derived exclusively from camera trap captures (Pfeffer et al. 2017). Because most of the observed species are solitary species we did not apply the group size function to the density equation (maximum average group size recorded was 1.06). We performed density calculations in R version 4.0.3 (R Core Team 2013) bootstrapping with 1000 iterations from the original data.

Camera trap distance sampling method

The CTDS method, developed by Howe et al. (2017), follows the standard point transect methods (Buckland et al. 2001) and each camera station is considered a sample point. Density (D) is estimated as,

$$\widehat{D} = \frac{\sum_{k=1}^{K} n_k}{\pi w^2 \sum_{k=1}^{K} e_k \hat{P}_k}$$

where, k = the camera station/point

K = set of camera stations/points

n = number of captures

w = truncation distance beyond which any recorded distances are discarded

e_k= effort expended at point k

$\hat{P}_k$ = estimated probability of obtaining an image of an animal that is within θ and w in front of the camera at a snapshot moment

The effort is described by $e_k = \frac{\theta T_k}{2\pi t}$, multiplied by the activity level (a), yields the actual trapping effort as follows.

$$e_k = \frac{\theta T_k}{2\pi t} * a$$

θ = average detection angle

T_k = time period the camera was active

t = the time between two snapshot moments considered (within the video)

Detailed explanations of these equations are provided in Howe et al. (2017). We calculated the effort for each camera trap station for separate species and provided it as the input for effort in distance software. Because of low height of the camera mount, the w values exceeding 6.2m were less accurate. Therefore, we right truncated to a maximum of 6.2m and

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left truncated to 1m. We used the previously calculated *a* values (for REM) in this equation. Detection angle θ was estimated as 0.715585 radians. We recorded the distance between cameras and animals every three seconds in video captures, 24 h per day. Hence, parameter *t* applied in the above equation was three seconds. A special consideration was given for observations of reactivity to the cameras by the animals. In such cases, the latter part of the videos where animals unusually stayed extended time periods in front of the cameras were excluded from analysis. We used the "Distance 7.1" software package (Thomas et al. 2010) for density calculations. Half-normal and hazard rate candidate models of the detection function were tested setting the maximum adjustment parameter at one to reduce overfitting with overly complex models (Cappelle et al. 2021; Howe et al. 2019; Buckland et al. 2010, Marques et al. 2007). Fitted probability density and detection probability plots were inspected to ensure they were monotonically non-increasing (Cappelle et al. 2021, Howe et al. 2019). Competing models with sufficient goodness of fit were selected using AIC criteria.

We estimated variances in Distance 7.1 using the default analytic variance estimators based on detection probability and encounter rate (Fewster et al. 2009), and also from 1000 non-parametric bootstrap resamples of camera station data points (Cappelle et al. 2021; Howe et al. 2017; Buckland et al. 2001). Bootstrap density estimates were recorded separately. Coefficient of variation (CV) was obtained using the square root of the variance and the point estimates in all methods used.

Density estimations were compared statistically using the Wald test, with a test statistic *W* assessed on the chi-squared distribution with one degree of freedom (Palencia et al. 2021b; Wald and Wolfowitz 1940).

We calculated relative abundance index (RAI) as a crude estimate (Cappelle et al. 2021) for all species, especially to represent the less abundant species where sufficient samples were lacking to calculate density. RAI was calculated as encounters per hundred trap nights (Kalle 2013).

Results

Meso-carnivore assemblage and capture abundance

A total of 3,402 camera trapping days yielded 3,357 video captures of 69 different animal taxa including 658 video captures of meso-mammal carnivores. During this study in MONP, we recorded all 12 meso-mammal carnivore species (Annex I) found on the island. However, we captured only seven species in excess of 45 videos. The abundance of rusty spotted cats (n=4) (Fig. 3 A), jungle cats (n=5), common palm civets (n=2), and brown mongooses (n=10) was very low in the study site. Therefore, density calculations based on REM model were performed only for the remaining species: fishing cats (n=106) (Fig. 3 C), ruddy mongooses (n=302), stripe-necked mongooses (n=52) (Fig. 3 B), ring-tailed civets (n=118) (Fig. 3 D), golden palm civets (n=45) (Fig. 3 E), otters (n=46) and golden jackals (n=45). We estimated that these capture numbers are greater than, or closer, to the benchmark of 'around 50' captures recommended by Rovero et al. (2013) for REM density estimates. Density calculations for the same species were also conducted based on CTDS method.

Detection distances/movement speeds/day ranges, activity patterns and activity level

The average detection distance (ADD) value ranged from 1.90 – 4.07 m for the species considered. The rusty-spotted cat recorded the lowest distance value, while otter recorded the highest. In general, effective detection distance (EDD) values were greater than the observed ADD values except for golden palm civet (Table 1).

The movement speeds ranged from 0.72 - 3.42 km/h. The fastest moving species was the otter, followed by the golden jackal, resulting in high day ranges for those two species. The highest activity levels were shown by fishing cat and golden jackal indicating that they were active during a greater proportion of time when compared to other species. We observed that all mongoose species and golden jackals were diurnal while civet species and otters were nocturnal (Table 1; Fig. 4). Fishing cats were mostly nocturnal yet could also be observed during day time as well. Jungle cats and rusty-spotted cats were recorded mostly at night. The highly nocturnal golden palm civet was the least active species. In addition, we observed this species to be the second slowest, recording the lowest day range (3.47 km/day).

Comparison of REM and CTDS density estimates

Based on Wald test statistic, any of the density estimates obtained from different methods of analyses were not significantly different for any of the species (*p>0.05*). However, the density estimates of fishing cat (Wald test: CTDS vs. REM: $W = 0.91$, $p = 0.34$) and ring-tailed civet (Wald test: CTDS (b) vs. REM: $W = 2.06$, $p = 0.15$) obtained using REM were relatively higher than CTDS estimates (Table 2). Ruddy mongooses had the highest abundance, and it was among the highest density estimates in all three analyses. However, the

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REM density estimate of ring-tailed civet was the highest recorded density. Lowest densities were recorded for otter and golden jackal. Density estimates derived using the CTDS method generally yielded lower figures when compared to the REM method (except on two occasions) (Table 2). However, the coefficient of variation (CV) values were generally higher in the CTDS method compared to REM (except in one occasion) (Table 2). The low abundance of rusty-spotted cat, jungle cat and brown mongoose were indicated by very low RAI values (Table 2).

Discussion

Our findings show that MONP is a protected area with a rich assemblage of meso-mammal carnivores (Annex I). However, when Felid species were considered, there were very few jungle cat and rusty-spotted cat camera trap sightings inside the study area of MONP. Because of the low number of captures of those two species, we were unable to calculate population densities using the REM or CTDS. However, RAI values of jungle cat and rusty-spotted cat were the lowest among the species on which we focused. The limited number of records of rusty spotted cats and jungle cats were from dense dry mixed evergreen forests and shrublands respectively, conforming the findings of Bora et al. (2020), Chatterjee et al. (2020) and Palei et al. (2019) on these cats' habitat occupancy. Based on our field observations, we posit tentatively that one reason for the low abundance could be that these two species are attracted to agricultural areas (paddy fields) and habitat edges, alternative habitats with abundant small mammal prey used by both species (Dharmarathne, personal communication, 2021; SCAR 2021; Bora et al. 2020; Miththapala 2018; Šálek et al. 2010; Nekaris 2003). In contrast, our results indicate that MONP is home to a healthy population of fishing cats, the largest of the three felid species studied. The fishing cat population densities recorded in this study are among the highest densities recorded for the species compared to research in other countries (Mishra et al. 2018; Sathiyaselvam et al. 2016). The large Maduru Oya reservoir and other reservoirs within the park provide ample food for this carnivore that is associated with water (SCAR 2021; Ganguly and Adhya 2020; Hunter 2019; Miththapala 2018; Mukherjee et al. 2016). The frequent release of fingerlings to the Maduru Oya reservoir by the local community-based fishing society and the abundance of fish and aquatic avifauna in its habitats make MONP an ideal site for fishing cats through the provision of food resources (Ganguly and Adhya 2020; Hunter 2019; Cutter 2015; Kitchener et al. 2010; Haque and Vijayan 1993).

Our results show that density of otters was relatively low, although this is another species that prefers aquatic fauna as its main prey (Dettori 2021; Romero and Guitián 2017; Bouros and Murariu 2017; de Silva 1996; Carss 1995). Although their population density (maximum estimate 0.16 per km^2) is similar to estimations from other studies (Quaglietta et al. 2015; Hájková et al. 2009; Lanszki et al. 2008), there may be a foraging niche overlap with fishing cat given their known food habits (Dettori 2021; Ganguly and Adhya 2020; Hunter 2019; Cutter 2015; de Silva 1996; Kitchener et al. 2010; Carss 1995; Haque and Vijayan 1993).

This is likely the first effort of estimating the densities of civets and mongooses in a wild habitat in Sri Lanka. The grey mongoose, which is thought to be common in the northern third of the island (Wijeyeratne 2008), was not captured in camera traps, although through direct visual observations, we spotted a couple of individuals. Santiapillai et al. (2000) and Wijeyeratne (2008) have reported a similar situation from Yala National Park, which is another protected area situated in the dry zone of the country. The brown mongoose abundance in MONP was low. The density of stripe-necked mongoose was moderate. We obtained high population density estimates among all focal species for the ruddy mongoose, which was also the dominant mongoose species in MONP, as observed by Jayasekara and Mahaulpatha (2019). The ring-tailed civet was the Viverrid with the highest density, validating its least concern (LC) status in the National Red List (MOE 2012). The common palm civet density was not calculated because of the very low number of captures.

When the two main analysis methods (REM and CTDS models) are compared, the only contrasting result we obtained was the density of endemic golden palm civet. Golden palm civets are generally arboreal (Wijeyeratne 2008) and the camera traps capture them only when they are on the ground. Therefore, the speed estimation based on a 2D model becomes biased, because their vertical movements were not recorded through our camera arrangement. The slowness of golden palm civets on ground is indicated by our speed calculation of 0.89 km/h. Considering the above, we recommend that the CTDS estimates (0.80-0.97 individuals per km^2) in which speed is not a parameter, to be relatively more accurate for this species despite the drawback of not recording arboreal movements. However, the bias caused by not recording vertical movements would not be completely eliminated unless methodology is adapted to account for such complex scenarios. In general the CTDS method is considered more suitable for low abundant species (Palencia et al. 2021b).

The unusually high "speed parameters" generated for otter and golden jackal did not have an adverse impact on REM density estimation because we obtained similar densities from the CTDS method. We suggest estimating the day ranges of the above two species in the study area using another method/repeated method to confirm the values we received. However, according to Rowcliffe et al. (2012) and Palencia et al. (2019) the alternative methods such as telemetry often underestimate travel distances. Radio tracking studies of otter in other countries indicate that otters can cover long distances ranging from >20 – 100 km in a single day (Ruiz-Olmo 2001) and occupy large home ranges (Quaglietta et al. 2015). Therefore, the day range of 27.5 km observed in the present study could likely be accurate. Research focused on golden jackal in Sri Lanka remains scarce (Jayaratne and Seneviratne 2020) and the observed density value was within the density range observed by Šálek et al. (2014) in Balkan Peninsula.

Approximately similar density estimates generated by both analyses, despite REM estimates being slightly higher, conform the observations of Palencia et al. (2021b). Therefore, we recommend both REM and CTDS methods for the population density estimation for meso-mammal carnivores in tropical habitats. However, CV values of CTDS method were relatively higher than the REM values despite the similarities of density figures. Density estimates of species with CV values <40% are generally considered reasonable, and in recent research work, the effort has been to further increase the precision (Cappelle et al. 2021; Palencia et al. 2021b; Harris et al. 2020; Howe et al. 2019). According to Cappelle et al. (2021) CV values between 10-20% are more desirable. When the present study is considered, 61.9% of the CV values were <40% and 42.9% were <30%. According to recent research, the precision can be further increased by increasing the sampling effort in different ways (Cappelle et al. 2021; Rovero et al. 2013). Hence, in order to obtain a greater number of capture events, we suggest following the recommendations of Cappelle et al. (2021); (a) increase the number of camera stations or (b) increase the length of sampling period. However, there remains the logistic concerns that are associated when camera trapping extremely rare species. We suggest the length of sampling period to be increased while deploying the appropriate number of camera stations as the best way forward. The moving survey method we followed also reduced the limitation occurred by low number of cameras, increasing the effort and precision.

Accounting for overdispersion with more customized model selection criteria as described by Howe et al. (2019) would increase the accuracy and precision of CTDS results. We identified that proper estimation of movement speed, activity and ultimately the day range of species was critical for the final density results of REM. Application of recently developed method by Palencia et al. (2019) integrating the behaviors and speed-ratio in calculations makes it possible to obtain unbiased day range values. Furthermore, with the development of machine learning techniques (Palencia et al. 2021a) and specialised "R packages" like "*trappingmotion*" (Palencia 2020) the analysis process will be streamlined. However, dealing with multiple species, we observed that number of encounters need to be higher in order to apply this method. When monitoring gregarious species, it is recommended to consider applying the group size function in the density equations (Rowcliffe et al. 2008). During the present study, the ruddy mongoose and the golden jackal were the species with the highest average group size with a value closer to one (1.06). Therefore, we did not include group size in the analyses.

We used a modified distance measuring method for this study, which saved the time and effort during field work and further helped to obtain accurate measurements during analyses. However, we would like to highlight that if the distance grid and table are used, camera height and orientation should be positioned precisely. In addition, based on the camera mounting height, this distance grid and table can be generated easily prior to camera trap deployment in the field. It is also important to note that the focal distance of the camera may differ from one model to another. When using different camera models, model specific distance calculations should be used. This method is less applicable in complex field situations with slope and rugged terrain. In those instances, original distance measuring techniques or slope adjusted parameters can be used. Both REM and CTDS methods require reasonable amount of field effort as well as substantial amount of time for processing the images/videos and exploratory analyses (Palencia et al. 2021b). We would like to highlight the requirement of suitable software for image and especially video processing. Integration of such software with machine learning would greatly reduce the time required in computer analyses.

The type of camera flash also has an impact on the behaviour and the movement speed of the animals. We highly recommend a no glow flash model such as Browning Dark OPS HD Pro, which causes minimum interference to the animals when REM and CTDS methods are used. However, we observed that the low glow flash Browning Strike Force HD Pro also interfered less, except for a few observations which we had to discard the capture records as behavioural changes were observed. Selection of these flash types also increases the battery

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life of cameras (one set of batteries usually lasted more than two months on video mode during our study). We do not recommend white flash camera models. Most of the focal species did not react to the cameras in a greater proportion of encounters. However, there were several instances where fishing cats and ring-tailed civets were observing the cameras in an enthusiastic nature where we had to discard some parts of the videos. Though not focused on in this study, elephants were highly reactive to the cameras and were often found attacking them. The use of videos (Cappelle et al. 2021; Howe et al. 2017) – instead of snapshots used in early REM and CTDS based studies (Pfeffer et al. 2017; Rovero and Marshall 2009) – improves the accurate identification of species. Moreover, the ability to observe the actual behaviour of the animal helps to determine when reactive behaviours take place. This also helped us to identify resting places of animals, which led to redeployment of two camera stations. Because we assessed multiple meso-carnivore species in this study, there was the concern of selecting a camera height that suits all species. Based on our observations, the increase in species shoulder height did not adversely impact the detection or encounter rate. Sometimes, the species could be identified even when some parts of the animal were out of the frame (for example the Jackal). We selected the height of 25cm to reduce the bias caused by not encountering the smaller animals when they are very close to the camera (for example the rusty-spotted cat). Therefore, the selection of camera height should be based on the morphometrics of the focal species. The availability of in-built display with video playback option was very useful during routine observations in the field. In addition, with videos, the movement speed estimation becomes more accurate because the bias caused by the delay between the snapshots is removed. Even though the methods followed during our work would have reduced the bias of animal reactivity and other technical concerns, we acknowledge that they were not eliminated completely.

Our study provides population density estimates for the meso-mammal carnivore species in MONP, which would inform future conservation and management decision-making and also a template by which their status could be assessed in forest habitats in other parts of the island. Additional parameters such as movement speed, activity patterns, activity level and day range that we generated can be also used for future research in a broad range of applications. The study shows clearly that REM and CTDS methods can be applied practically under field conditions of tropical forests, to assess multiple species. The recommendations for modifications to build upon original methodologies and analyses will improve efficiency and cost-effectiveness of similar research in the future.

Conclusions

The study identifies MONP as a protected area with a rich meso-mammal assemblage. However, our study indicates that species such as rusty-spotted cat, jungle cat, brown mongoose, otter and golden jackal have low abundances and population densities. MONP sustains considerably healthy populations of fishing cats, ring-tailed civets and ruddy mongooses. The two main population estimation methods we used, the REM method and CTDS method could be applied successfully in the forest habitats of Maduru Oya. The CTDS method was more easily applicable in the field with suggested modifications of distance estimations. However, the relatively complex REM method can be more useful as it generates additional information such as activity, day range and movement speed which are useful for other ecological studies and decision making.

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Author contributions

Dharshani Mahaulpatha, Dulan Jayasekara and Sriyanie Miththapala conceived the study. Dulan Jayasekara and Dharshani Mahaulpatha devised the methodology and established the camera stations. Dulan Jayasekara analyzed the data with input from Dharshani Mahaulpatha and Sriyanie Miththapala. Dulan Jayasekara led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

Authors declare no competing interests

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Table 1: Additional parameters derived for density calculations. ADD: average detection distance; EDD: effective detection distance**;** Speed of animal movement; Activity pattern (sD = strictly diurnal; sN = strictly nocturnal; mD = mainly diurnal; mN = mainly nocturnal; Activity level: the proportion of the day a species is active); Day range: daily distance travelled; IUCN status (IUCN, 2021).

Species	ADD (m)	EDD (m)	Movement Speed (km/h)	Activity Pattern	Activity level	Day range (km/day)	IUCN status (Global)
Fishing cat *Prionailurus viverrinus*	2.54	2.75	0.72	mN	0.461	7.96	VU
Rusty-spotted cat *Prionailurus rubiginosus*	1.9	-	-	mN	-	-	NT
Jungle Cat *Felis chaus*	2.62	-	-	mN	-	-	LC
Ring-tailed civet *Viverricula indica*	2.84	3.19	1.02	sN	0.288	7.05	LC
Golden palm civet *Paradoxurus zeylonensis*	3.01	2.89	0.86	sN	0.161	3.34	LC
Stripe-necked mongoose *Urva vitticollis*	3.11	3.35	1.22	sD	0.288	8.39	LC
Ruddy mongoose *Urva smithii*	2.91	3.47	1.84	sD	0.390	17.22	LC
Brown mongoose *Urva fuscus*	2.92	-	-	sD	-	-	LC
Otter *Lutra lutra*	4.07	4.92	3.42	mN	0.353	28.97	NT
Golden jackal *Canis aureus*	3.35	3.97	3.10	mD	0.419	31.13	LC

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Table 2: Density estimates of meso-mammal carnivore species in MONP using three analytical methods: REM, conventional CTDS and bootstrap CTDS(b) density estimates. (Density is given as individuals/km^2, LCL=Lower Confidence Limit; UCL=Upper Confidence Limit; %CV=percent Coefficient of Variation). CTDS model function: half normal - (hn), hazard rate - (hr). RAI: Relative Abundance Index.

Species	RAI	Density Esitmate Method	Density (individuals per km^2)			
			Estimate	LCL	UCL	% CV
Fishing cat *P. viverrinus*	3.11	REM	**1.54**	0.82	2.39	29.0
		CTDS(b) (hr)	**1.13**	0.45	2.90	50.1
		CTDS (hr)	**0.90**	0.51	1.60	29.8
Rusty-spotted cat *P. rubiginosus*	0.12	-	-	-	-	-
Jungle cat *F. chaus*	0.15	-	-	-	-	-
Ring-tailed civet *V. indica*	3.47	REM	**2.28**	1.13	3.57	35.8
		CTDS(b) (hr)	**1.91**	1.03	3.55	31.9
		CTDS (hr)	**1.69**	1.09	2.63	22.6
Golden palm civet *P. zeylonensis*	1.32	REM	**1.69**	1.17	2.29	20.8
		CTDS(b) (hn)	**0.80**	0.32	1.98	48.6
		CTDS (hn)	**0.97**	0.42	2.24	44.2
Stripe-necked mongoose *U. vitticollis*	1.53	REM	**0.75**	0.47	1.06	23.0
		CTDS(b) (hr)	**0.62**	0.32	1.22	34.9
		CTDS (hr)	**0.56**	0.34	0.93	26.1
Ruddy mongoose *U. smithii*	8.88	REM	**2.19**	1.48	2.95	21.3
		CTDS(b) (hr)	**2.32**	1.37	3.93	27.1
		CTDS (hr)	**2.23**	1.40	3.56	23.9
Brown mongoose *U. fuscus*	0.29	-	-	-	-	-
Otter *L. lutra*	1.35	REM	**0.15**	0.05	0.28	45.9
		CTDS(b) (hr)	**0.16**	0.07	0.36	45.0

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		CTDS (hr)	**0.15**	0.05	0.47	61.1
Golden jackal *C. aureus*	1.32	REM	**0.17**	0.07	0.27	39.1
		CTDS(b) (hn)	**0.16**	0.60	0.42	51.67
		CTDS (hn)	**0.16**	0.07	0.40	48.5

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Figure 1: Map of Maduru Oya National Park with the study area and camera station locations. Location of the park in the map of Sri Lanka is also shown

Figure 2: The distance grid superimposed on camera trap capture frame to estimate distances

Figure 3: (A) Rusty-spotted cat, (B) Stripe-necked mongoose (C) Fishing cat (D) Ring-tailed civet and (E) Golden palm civet captured in our camera traps

Figure 4: Activity patterns of fishing cat, ring-tailed civet, ruddy mongoose and golden jackal in MONP, as captured by distributions of camera-trap records. Black steps are observed frequencies, and curves are fitted circular kernel distributions

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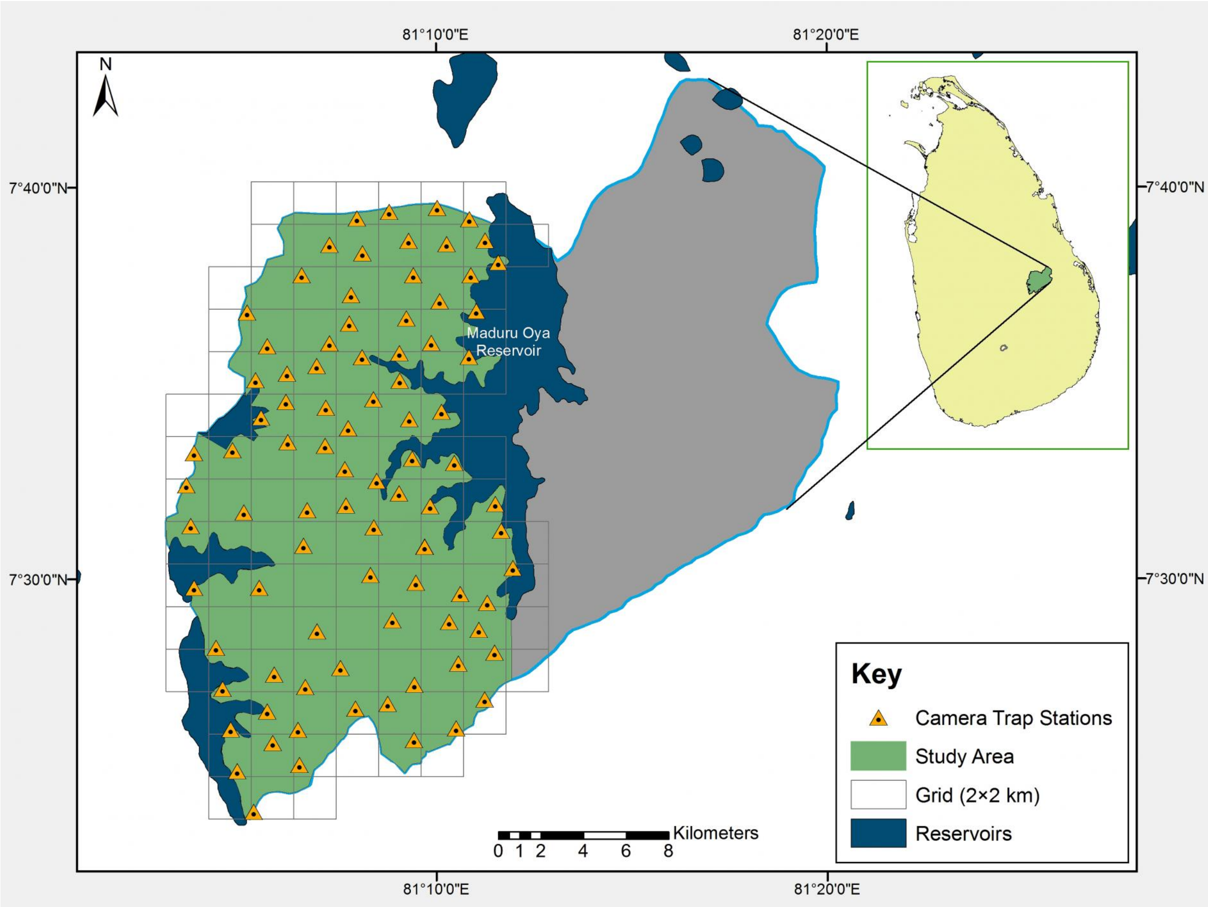

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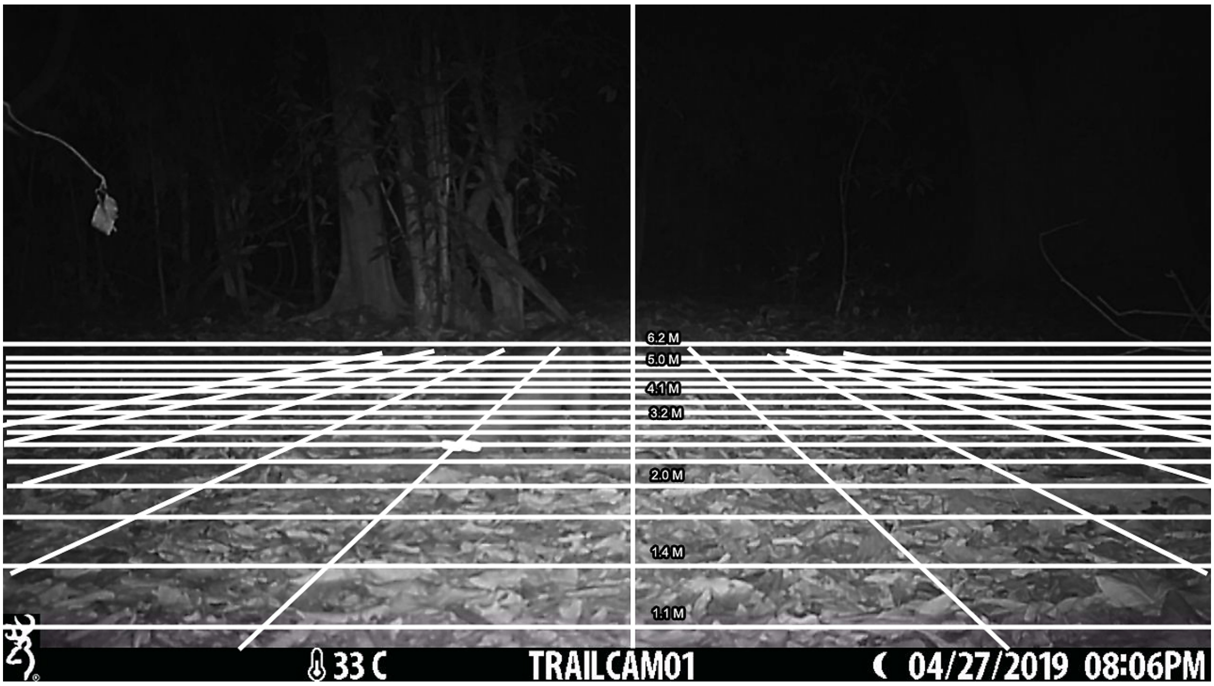

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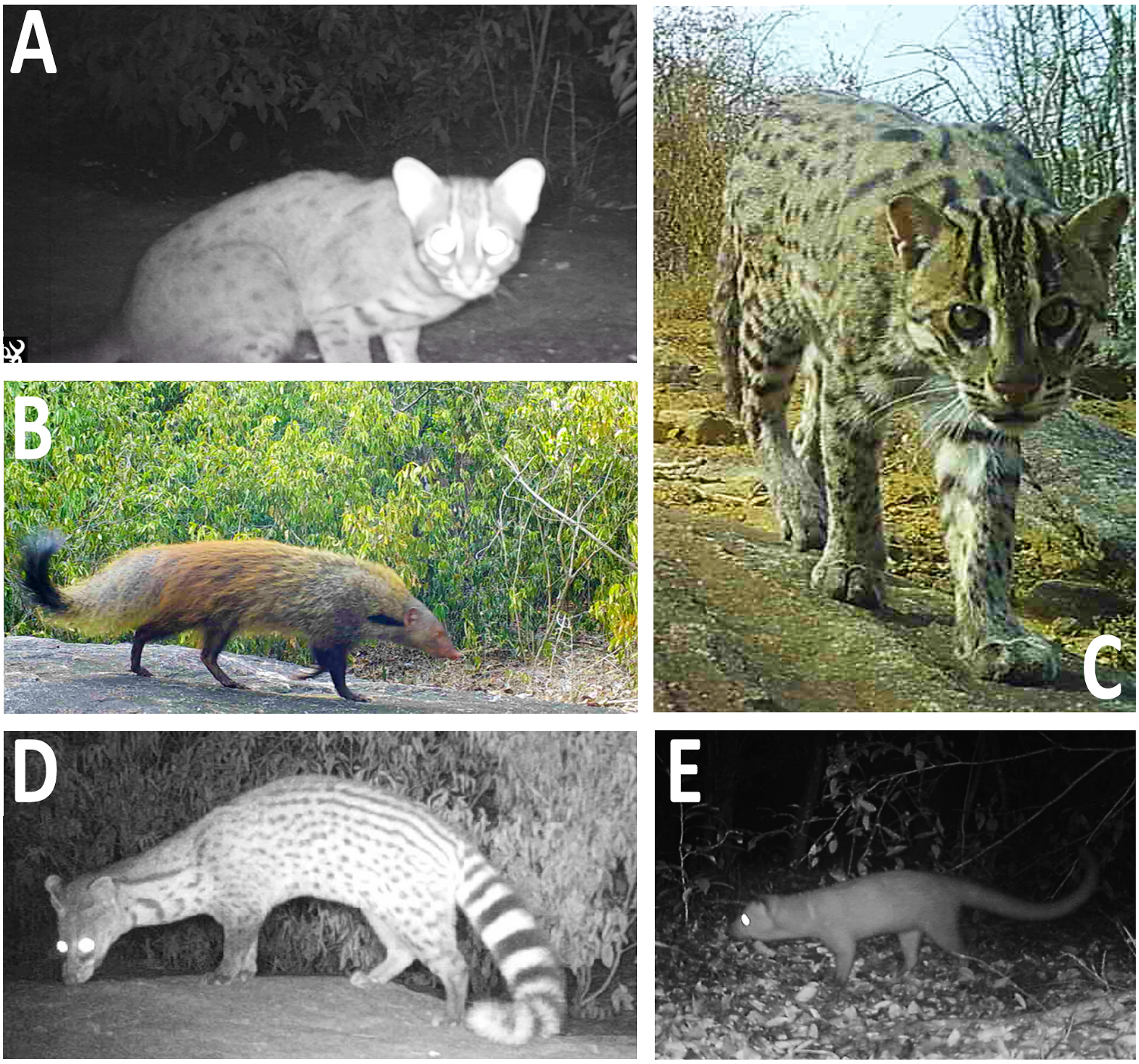

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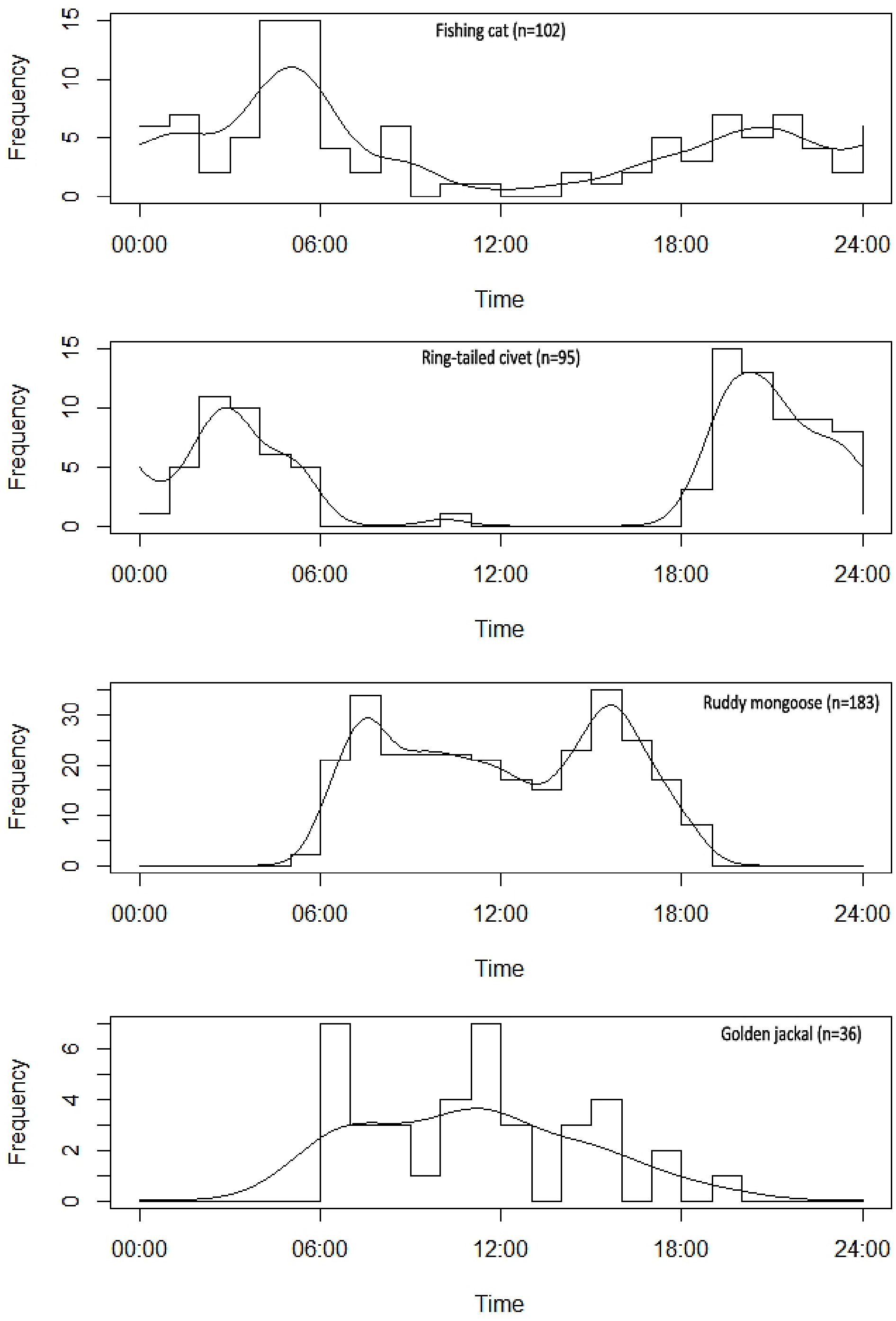

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Supplementary Online Material

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