



Seasonal Differences in the Encounter Rate of the Fat-Tailed Dwarf Lemur (*Cheirogaleus medius*) in the Transitional Forests of Northwest Madagascar: Implications for Reliable Population Density Assessment

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Received: 8 August 2022 / Accepted: 14 February 2023 / Published online: 27 February 2023
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Abstract

Primate encounter rates often vary throughout the year due to seasonal differences in activity, ecology, and behaviour. One notably extreme behaviour is continuous hibernation. Although a rare adaptation in primates, the dwarf lemurs of Madagascar (genus *Cheirogaleus*) enter obligate hibernation each year during the dry season, after spending the wet season consuming high-energy foods. Whilst seasonal changes in activity in some *Cheirogaleus* populations are well-known, many species remain little-studied, and there is no specific information on their encounter rates, nor when they enter and emerge from hibernation. This uncertainty critically affects reliable calculation of population density estimates for these highly threatened lemurs. In this study, we assessed how encounter rates of the fat-tailed dwarf lemur (*C. medius*) vary seasonally in the transitional forests of the Sahamalaza-Iles Radama National Park, northwest Madagascar, during a 4-year period. We established a system of line transects ($N=60$) throughout our study area, on which we conducted distance sampling of *C. medius*. We then used our distance sampling data to calculate encounter rate and population density data. We found encounter rates of *C. medius* to be significantly higher during the wet season compared with the dry season. Furthermore, encounter rates of *C. medius* were particularly low from May–August. These results provide some evidence to suggest the time period that *C. medius* hibernate in Sahamalaza-Iles Radama National Park. These findings underpin the importance of careful study design when surveying threatened species with seasonal differences in activity, such as those that hibernate. This study also demonstrates the importance of species-specific behavioural data for accurate population density assessment, which is required to inform conservation action.

Handling Editor: Addisu Mekonnen

Keywords Environmental hardship · Hibernation · Line transect · Population density · Sahamalaza · Seasonality

Introduction

Primate encounter rates often vary profoundly between seasons (Branch, 1983; van Schaik & Brockman, 2005). This is because seasonal differences in primate activity levels (Erkert & Kappeler, 2004), feeding ecology (Hanya & Chapman, 2013; Poulsen *et al.*, 2001), ranging (Reyna-Hurtado *et al.*, 2018), and social behavior (Heldstab *et al.*, 2021) can affect our ability to observe and detect wild primates at different times of the year. Whilst primate encounter rate data can be collected for the whole year to calculate the most reliable population density estimates, this often is not possible due to the remote location of many primate populations and the limited financial resources available to conduct such studies (Cowlshaw & Dunbar, 2021; Turner & Corlett, 1996). Because accurate and reliable data on primate population densities are required for their conservation, primate studies need to be carefully planned to avoid periods when primate observation and detection rates are likely to be lower due to certain behaviors.

Torpor, the act of entering into a state of physical inactivity, is one such adaptation that impacts seasonal detection rates in some primate species (Miller *et al.*, 2018). Seasonal torpor is a rare and extreme adaptation among primates (Lyman *et al.*, 1982; Schülke & Ostner, 2007), and this is primarily because most species of primates live in the tropics where seasonal variations in temperature are less profound (Lovegrove, 2003). With the exception of the small-bodied tamarins (Moynihan, 1970), all documented cases of primate torpor occur in nocturnal strepsirrhine species that have a body mass of less than 600 g (Dausmann & Warnecke, 2016). Many primate taxa that undergo torpor employ only daily torpor in times of low food and water availability (Dausmann & Warnecke, 2016; Perret & Aujard, 2001). This is a well-known trait in mouse lemurs (genus *Microcebus*) (Kobbe *et al.*, 2011; Lovegrove *et al.*, 2014; Ortman *et al.*, 1997; Schmid, 2000), but it also occurs in the Javan slow loris (*Nycticebus javanicus*), the African lesser bushbaby (*Galago moholi*), the hairy-eared dwarf lemur (*Allocebus trichotis*), and possibly Coquerel's giant mouse lemur (*Mirza coquereli*) (Dausmann, 2014; Dausmann & Warnecke, 2016; Nowack *et al.*, 2010). However, some strepsirrhines, such as the dwarf lemurs of the *Cheirogaleus* genus (Dausmann & Warnecke, 2016), the pygmy slow loris (*N. pygmaeus*) (Ruf *et al.*, 2015), Goodman's mouse lemur (*M. lehilahytsara*) (Andriambelosen *et al.*, 2020), the reddish-gray mouse lemur (*M. griseorufus*) (Kobbe *et al.*, 2011), and the brown mouse lemur (*M. rufus*) (Atsalis, 1999) enter torpor for prolonged periods of several days or months (hibernation) if they are able to store enough energy reserves. Studying such species is therefore difficult, because they are inactive and undetectable for long periods of the year.

The dwarf lemurs (genus *Cheirogaleus*) are a group of nine, small, omnivorous, primate species from Madagascar (Groves, 2016; McLain *et al.*, 2017) and are the sole group of primates that enter obligate hibernation (Dausmann, 2008; Dausmann & Blanco, 2016; Wright & Martin, 1995). To do this, *Cheirogaleus* spp. spend much of their active periods feeding and building up reserves of fat in order to survive periods of

food and water shortages during the dry season (Dausmann & Blanco, 2016). *Cheirogaleus* are distributed throughout Madagascar and are present in a range of habitat types, including dry forest (e.g., the fat-tailed dwarf lemur (*C. medius*): Dausmann *et al.*, 2005), humid forest (e.g., the greater dwarf lemur (*C. major*), the Montagne d'Ambre dwarf lemur (*C. andysabini*): Lahann, 2007; Dausmann, 2013; Lei *et al.*, 2015), central highland and montane forest (e.g., Crossley's dwarf lemur (*C. crossleyi*), Sibreei's dwarf lemur (*C. sibreei*): Blanco *et al.*, 2008; Blanco & Godfrey, 2014), and transitional forests that have characteristics of both humid and dry forests (e.g., *C. crossleyi*, Sheth's dwarf lemur (*C. shethi*): Hending *et al.*, 2017a). They also have been observed in agroecosystems (Hending *et al.*, 2018; Webber *et al.*, 2020). Habitat structure and resource availability vary considerably among these habitat types, and differences in encounter rates, behavior, ecology, and hibernation length have been described for different *Cheirogaleus* species from different forest types and between different bioclimatic zones (Dausmann & Blanco, 2016). Information on *Cheirogaleus* is generally lacking, and our knowledge of species-specific encounter rates and hibernation duration is generally restricted to just a few studies from only one or two study locations (e.g., *C. major* in eastern Madagascar: Lahann, 2007; Blanco *et al.*, 2018). Because some species of *Cheirogaleus* have large geographic distributions in multiple habitat types and climatic zones (Frasier *et al.*, 2016), we therefore have no knowledge of when many *Cheirogaleus* populations enter and emerge from hibernation. As *Cheirogaleus* encounter rates are certain to vary seasonally due to hibernation periods, this limits our ability to study *Cheirogaleus* behavioural ecology and constrains the period in which we can reliably carry out population assessments.

With a seasonally fluctuating mean body size of 150–270 g, *Cheirogaleus medius* is one of the smallest *Cheirogaleus* (Fietz & Ganzhorn, 1999), and, like other *Cheirogaleus*, it has the ability to store fat reserves as adipose tissue in its tail. This adaptation allows *C. medius* to hibernate for periods of up to 8 months, the longest for any primate (Dausmann & Blanco, 2016). *C. medius* has a very large, discontinuous geographic distribution, and it inhabits the dry forests of the west of Madagascar and the transitional forest of the Sambirano Domain in the northwest. The hibernation duration of this species has thus far been studied in only dry and littoral forest habitat (Dausmann & Blanco, 2016; Dausmann *et al.*, 2005; Lahann & Dausmann, 2011), and differences in hibernation length between these two habitat types have been documented, suggesting that this species has flexible life-history traits in relation to its environment (Lahann & Dausmann, 2011).

In this study, we investigated how encounter rates of *C. medius* vary among the wet and dry season in transitional forests of the Sahamalaza-Iles Radama National Park, northwest Madagascar, to gain insight into the hibernation schedule of this species. We also aimed to improve survey methods and study-planning for *C. medius* to obtain reliable density estimates. As the hibernation schedule of this species is likely to affect detection rates, and therefore population density estimates, we predicted that detection rates would vary significantly between the wet and dry seasons. As hibernation duration differences have already been observed between dry and littoral forest due to climatic differences (Dausmann & Blanco, 2016; Lahann & Dausmann, 2011), we also predicted that *C. medius* hibernation would be different in transitional forest in comparison to the other two habitat types.

Methods

Ethical Note

All research complied with UK Home Office policies when working with animals and all research adhered to the legal requirements of Madagascar. Research in the Sahamalaza-Iles Radama National Park was permitted by Madagascar National Parks (Permit numbers 245/19 and 124/22 – MEEF/SG/DGGE/DAPRNE/SCBE. Re). We consulted the Code of Best Practices for Field Primatology when planning all methods undertaken in this study.

Data Availability

The datasets used during this study are available from the corresponding author on reasonable request.

Conflict of Interest

The authors declare that they have no conflict of interest.

Study Site

Sahamalaza-Iles Radama National Park (hereafter referred to as SIRNP) is located in North West Madagascar on the Sahamalaza peninsula, between 13°52'S – 14°37'S and 45°38'E – 48°04'E (Rode *et al.*, 2013). SIRNP is a UNESCO Biosphere Reserve and gained full National Park status in 2007 (Schwitzer *et al.*, 2007), yet despite this protection, it has undergone heavy deforestation in recent years (Seiler *et al.*, 2014). SIRNP now has only two remaining forests: the 1,169 ha Anabohazo continuous forest block and the highly fragmented 1,020 ha Ankarafa forest (Volampeno, 2009). Whilst a few smaller, highly degraded forest fragments do remain, scattered throughout the National Park, much of the area is now characterised by disturbed, anthropogenic savannah, grassland, and some remnants of scrub and gallery forest (Volampeno *et al.*, 2011). We conducted our study in both the forests of Ankarafa (14°22'S, 47°45E) and Anabohazo (14°19'S, 47°54'E) (Fig. 1).

SIRNP is located in the Sambirano Domain, an area of Madagascar that is characterized by subhumid transitional forest; the forests of SIRNP therefore encompass a mixture of deciduous and evergreen tree species, many of which are endemic to the Sambirano Domain (Du Puy & Moat, 1996; Koechlin, 1972). The climate of SIRNP is highly seasonal, with a separate hotter wet season (November–April) and a cooler dry season (May–October) (Mandl *et al.*, 2018). Mean temperature range in SIRNP is 20.6–32.0 °C, with recorded extreme temperatures of 13.2–39.1 °C (Hending *et al.*, 2017b; Volampeno *et al.*, 2011) and mean annual precipitation rates of approximately 1,600 mm (Schwitzer *et al.*, 2007).

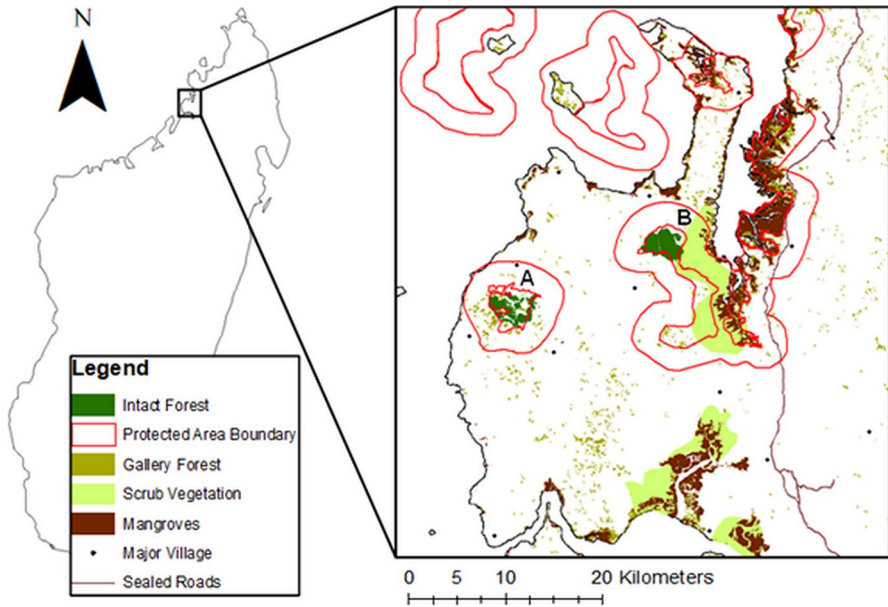


Fig. 1 The Sahamalaza-Iles Radama National Park, Madagascar, and the location of Ankarafa forest (A) and Anabohazo forest (B). Figure created in ArcMap, with a scale of 1:7,000,000 for Madagascar and a scale of 1:350,000 for the zoomed panel. The two red lines surrounding protected areas represent the protected area (inner) and a 3-km buffer zone (outer).

Distance Sampling

Between June 9, 2018 and May 13, 2022, we conducted line-transect distance sampling along several transects, a method regularly used for arboreal primates (Buckland *et al.*, 2010), to assess the encounter rates of *Cheirogaleus medius* in SIRNP. We established a total of 60 line transects in the forests of Ankarafa ($N=40$, mean length = 1,021 m, range = 525–1,525 m) and Anabohazo ($N=20$, mean length = 1,124 m, range = 500–1,500 m). Due to the large number of transects, we did not walk all transects each month. The Ankarafa transects were in 40 separate forest fragments (one transect per forest fragment). We began each transect walk at approximately 19:00, when *C. medius* would be actively feeding (Fietz & Ganzhorn, 1999; Müller, 1999). During each transect walk, two researchers and one guide walked along the transect at a steady and continuous pace of approximately 1 km/h. The same three participants conducted all transects to avoid observational bias (Buckland *et al.*, 2001). We used high-lumen handheld torches (EC20, Nitecore, Guangzhou, China) and headlamps (Tikkina and Tikka+, Petzl, Crolles, France) to spot any *C. medius* individuals that were present along the transect based on eye-shine. For any sighted *C. medius* individuals, we recorded their geographic position using a handheld GPS (eTrex 30, Garmin, Olathe, KS), the date and time of the observation, and we measured the perpendicular distance from the transect line to the tree in which the lemur was positioned using a handheld laser measure (80 m, XCSOURCE, San Francisco, CA). Despite the

high density of the vegetation at the study site, we were able to distinguish *C. medius* from the sympatric Sahamalaza sportive lemur (*Lepilemur sahalalaza*) by their pelage colouration and size differences (Mittermeier *et al.*, 2008). Furthermore, we could distinguish *C. medius* from the sympatric northern giant mouse lemur (*Mirza zaza*) and the Sambirano mouse lemur (*Microcebus sambiranensis*) by their size and movement; locomotion of *C. medius* is slower than that of *M. zaza* (Müller & Thalmann, 2002; Rode-Margono *et al.*, 2016) and *C. medius* is larger than *M. sambiranensis* (Mittermeier *et al.*, 2008). Although our study took place over almost 4 years, we did not conduct any transect surveys during December due to the inaccessibility of the site around this time.

Encounter Rates and Population Density Estimates

We calculated monthly mean encounter rates for this study, by dividing the number of observed individuals for each transect by the total transect distance (N/km). We then calculated mean *C. medius* encounter rate for each transect across all repeat walks, for both forests individually and for SIRNP as whole. We also calculated mean *C. medius* encounter rates for each month across transects. We submitted our *C. medius* count data, transect length values and perpendicular distance values (Supplementary File 1) to the Distance 7.5 software (Thomas *et al.*, 2010) to quantify transect survey effort (estimated strip width: ESW—the area under the distance function from its left-truncation limit to its right-truncation limit) and to calculate *C. medius* population size and density, with lower and upper 95% confidence limits, for SIRNP. We used the Buckland method to calculate our population densities (Buckland *et al.*, 2001), as it has been used successfully in other lemur population studies (Axel & Maurer, 2011; Quémère *et al.*, 2010) and because it accounts for the decreasing probability of observing our study species as its perpendicular distance from the transect increases. We used instance detection functions, and we truncated our datasets with a 5% threshold to remove very distant observations. We also used Distance to estimate the population size for *C. medius* with lower and upper 95% confidence limits using our population density values and the area of each surveyed forest. Forest area was determined before this study with GPS waypoint data obtained during perimeter walks; forest area was later calculated using ArcGIS (Version 10.6.1, Esri, Redlands, CA).

Extraction of Temperature and Precipitation Variables

We used R Studio (R.Studio, Inc., Boston, MA) packages “raster” (Hijmans, 2019) and “rgdal” (Bivand *et al.*, 2019) to download average monthly temperature and precipitation variable data for SIRNP for our study period (2018–2022) directly from the WorldClim global climate database (Fick & Hijmans, 2017). Specifically, we downloaded mean monthly data for average temperature, minimum temperature, maximum temperature, and precipitation. When specifying the parameters of our

variable extraction, we used the GPS point corresponding to the midpoint of our study area (latitude = -14.3881 , longitude = 47.8540), and we used the highest possible raster resolution (1-km^2 tiles) to obtain the most accurate and localized data possible (Fig. 2).

Data Analysis

We performed all statistical analyses in R Studio with an α -level of 0.05. Our monthly encounter rate data for each transect was of normal distribution (Shapiro–Wilk normality test: $w=0.884$, $P=0.116$), so we compared how *C. medius* encounter rates vary between months by using a chi-square test. To investigate the relationship between *C. medius* encounter rate and temperature and precipitation, we first subjected the temperature and precipitation variables (independent variables) to tests of residual normality and homoscedasticity with the “olsrr” package (Hebbali, 2018). We investigated the relationship between *C. medius* activity levels and temperature and precipitation with individual Spearman’s rank correlation tests. To compare *C. medius* population density and size between the wet season (November–April) and dry season (May–October), we created a separate dataset of mean encounter rates for only the transects that we surveyed during both seasons (we removed transects surveyed in only the wet or dry season and excluded them from this dataset). The mean encounter rates dataset did not meet the assumptions of parametric analyses (Shapiro–Wilk normality test: $w=0.776$, $P=0.005$), and so we compared mean encounter rates between the two sampling periods (wet season

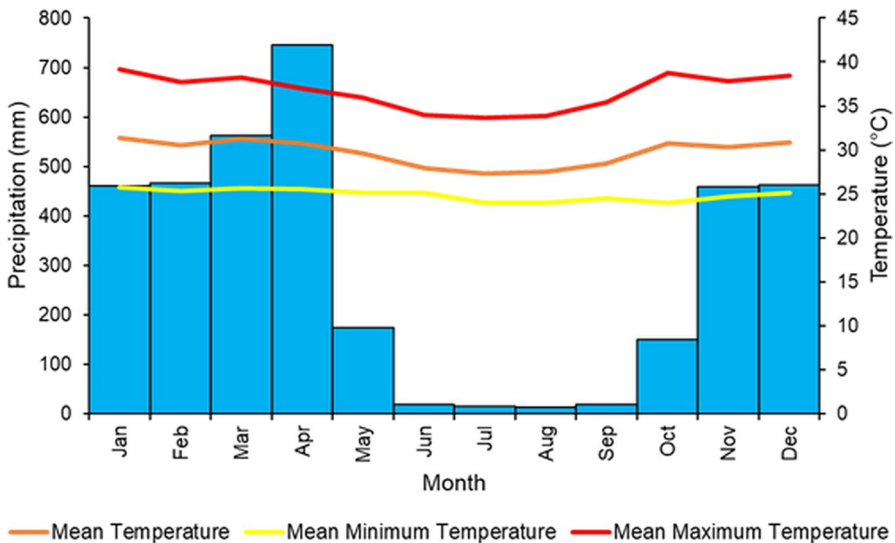


Fig. 2 Precipitation and temperature of the Sahamalaza-Iles Radama National Park, Madagascar, for February 2018–May 2022. Precipitation represents the total rainfall for each month. Figure created using data downloaded from the Worldclim database (Fick & Hijmans, 2017).

transects $N=84$, dry season transects $N=160$) with a paired Wilcoxon test (one mean encounter rate value per transect for both the wet and dry season).

Results

Encounter Rates

We performed a total of 264 transect surveys across our 60 established transect lines (mean=4.40 walks per transect, range=1–10), with a total survey distance of 275.30 km. During our study, we observed a total of 130 *Cheirogaleus medius* individuals, a mean of 0.49 individuals per transect walk (0.47 per km). The encounter rates of *C. medius* were significantly uneven among the months that were surveyed (chi-square test: $\chi^2=504.91$, $df=207$, $P<0.001$; Fig. 3). Specifically, we observed the lowest encounter rates of *C. medius* from May to August.

The mean encounter rate of *C. medius* was significantly positively correlated with monthly mean temperature (S (test statistic)=69.658, ρ (correlation coefficient)=0.683, $P=0.020$) and mean maximum temperature ($S=50.000$, $\rho=0.773$, $P=0.008$). However, *C. medius* encounter rate did not correlate significantly with monthly mean minimum temperature ($S=135.030$, $\rho=0.386$, $P=0.241$) and precipitation ($S=148.000$, $\rho=0.327$, $P=0.327$; Fig. 4).

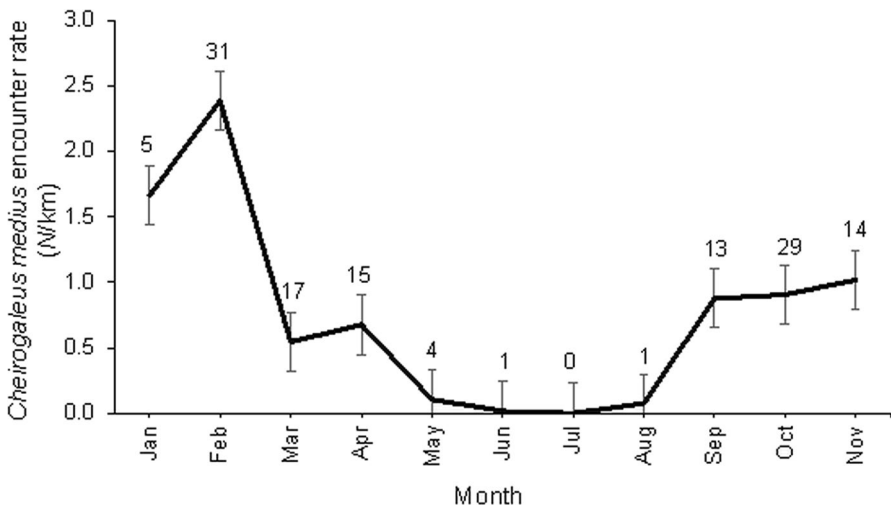


Fig. 3 Mean monthly encounter rates, with standard error (error bars), of *Cheirogaleus medius* in the Sahamalaza-Iles Radama National Park, Madagascar, during the study period June 2018–May 2022, with sample sizes of *C. medius* individuals (N) observed for each month.

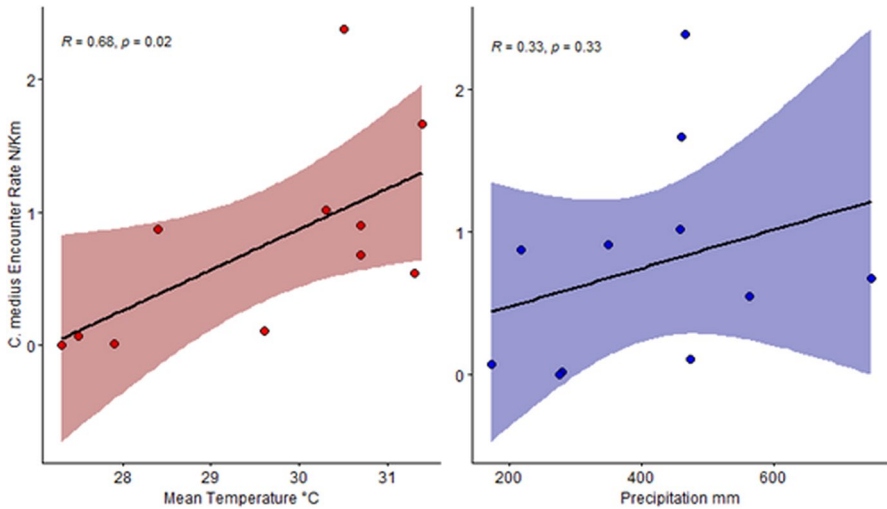


Fig. 4 Data and Spearman's correlation test results of mean monthly temperature and precipitation against *Cheirogaleus medius* encounter rate, with 95% confidence intervals, in the Sahamalaza-Iles Radama National Park, Madagascar, June 2018–May 2022.

Population Density and Size Estimates

The population density and size estimates for *C. medius* were profoundly different between the data collected for the wet and dry seasons (Fig. 3; Table I). Our statistical analysis of transect mean encounter rates also show a significant difference between the two periods (paired Wilcoxon test: $V=66$, $P=0.034$), with encounter rate being higher during the wet than dry season.

Discussion

Seasonal Differences in Encounter Rates

Although we observed *Cheirogaleus medius* individuals throughout the whole study period, our encounter rates were significantly higher in the wet season than in the dry season (Fig. 3). These findings are certainly due to lower activity levels of *C. medius* during the dry season, as many individuals would have been hibernating, and these observations are important for the planning and organisation of future studies into this species at this site. As has been suggested for the populations of *C. medius* in dry forest habitat (Dausmann *et al.*, 2005), *C. medius* activity may be lower during the dry season due to lower water and food availability and lower temperatures; we also observed *C. medius* less frequently during times of the year with low precipitation (although this difference was not significant) and lower temperatures in this study, as demonstrated by our correlation analyses

Table 1 The encounter rate, estimated population densities (mean number of individuals per kilometre squared (lower and upper 95% confidence limits)), and abundance (estimated mean population sizes (lower and upper 95% confidence limits)) of *Cheirogaleus medius* in two surveyed forests of the Sahamalaza-Iles Radama National Park, Madagascar, and for the protected area as a whole, June 2018–May 2022. Values are presented for the dataset as a whole, and for the wet (November–April) and dry (May–October) seasons separately

	Site	Area (km ²)	Survey distance (km)	Individuals (N)	N/Km	Estimated strip width	Density (N/km ²)	Abundance
All data	Ankarafa	10.20	135.05	78	0.58	6.04	47.80 (33.6–68.00)	488 (342.76–693.6)
	Anabohazo	11.69	140.25	51	0.36	10.15	17.90 (9.10–35.10)	209 (106.38–410.32)
	Total	21.89	275.30	129	0.47	8.17	28.70 (19.20–42.80)	628 (420.28–936.89)
Wet season	Ankarafa	10.20	55.20	36	0.65	5.95	54.80 (34.00–88.40)	559 (346.80–901.68)
	Anabohazo	11.69	28.00	44	1.57	10.33	76.00 (46.40–124.60)	888 (542.42–1456.57)
Dry season	Total	21.89	83.20	80	0.96	8.28	58.10 (40.50–83.30)	1272 (886.55–1823.44)
	Ankarafa	10.20	79.85	42	0.53	7.01	37.50 (20.10–70.10)	383 (205.02–715.02)
	Anabohazo	11.69	112.25	7	0.06	10.13	3.10 (1.10–8.90)	36 (12.86–104.04)
Total	21.89	192.10	49	0.26	6.98	18.30 (9.30–35.80)	401 (203.58–783.66)	

(Fig. 4). However, our *C. medius* encounter rates were high in September and October (Fig. 3) when rainfall was still very low at our study site (Fig. 2). *C. medius* encounter rate therefore may not be fully dependent on climatic factors. The lack of significant correlation also may be related to inaccurate information on weather from the WorldClim datasets, because often the number of weather stations from which this information is collected are very limited in tropical regions. Species-specific behavioural ecology and the habitat-related and environmental causes for the onset and offset of hibernation are likely to provide a fuller explanation of why *C. medius* encounter rates vary between months and between seasons. As these factors often are site-specific and species-specific (Dausmann & Blanco, 2016), further research into *C. medius* ecology and natural history in SIRNP is required to provide a more comprehensive answer to our research question.

Insights into *Cheirogaleus medius* Hibernation

Encounter rates of *C. medius* were very low during the period May–August (Fig. 3), and these observations may indicate the period when *C. medius* enters hibernation in SIRNP. This period coincides with the lowest monthly rates of precipitation and the lowest annual temperatures (Fig. 2), which is supported by our Spearman's correlation analyses of temperature (Fig. 4). This potential hibernation period of four months is much shorter than that of *C. medius* in dry forest habitat (6–8 months: Dausmann & Blanco, 2016) but similar to that of the littoral forest habitat *medius*-like (Thomas's dwarf lemur, *C. thomasi*) populations (4–5 months: Lahann & Dausmann, 2011). As decreasing temperatures, low water availability, and food scarcity influence the hibernation patterns of *C. medius* (Dausmann *et al.*, 2005), these differences among habitat types are expected as the transitional forests of North West Madagascar have a higher annual rainfall than dry forest habitat (Donque, 1972). Although we observed six *C. medius* individuals during the period May–August, these lemurs may have been juveniles that were not able to accumulate the necessary fat reserves for longer hibernation (Blanco & Rahalinarivo, 2010). As *Cheirogaleus* have flexible life history traits (Lahann & Dausmann, 2011), it is likely that the climate of SIRNP has influenced the timing of when the resident *C. medius* populations enter hibernation.

C. medius is considered to have the highest hibernation duration of any of the *Cheirogaleus* species (Dausmann & Blanco, 2016). However, our encounter rate data for SIRNP suggest that some populations of *C. medius* may hibernate for shorter periods than the rainforest species *C. crossleyi* (3.5–5.5 months) and *C. sibreei* (4.5–7 months) (Blanco & Godfrey, 2014). These differences in hibernation duration may be due to the actual cause of the hibernation itself; hibernation expression in sympatric *C. crossleyi* and *C. sibreei* for example is interspecific due to species-specific ecology (Blanco & Rahalinarivo, 2010; Dausmann, 2013). This further supports the theory of flexible life history traits in relation to hibernation among *Cheirogaleus* (Dausmann & Blanco, 2016).

Population Density and Size

The population density of *C. medius* in SIRNP (Table 1) was similar to that reported in other studies of this species from the dry forest (20–200 individuals/km²: Hladik *et al.*, 1980; Fietz, 1999). *C. medius* population density also varied between the two forest sites that we surveyed in SIRNP (Table 1). *Cheirogaleus* may be sensitive to habitat degradation and edge-effects (Lehman *et al.*, 2006; but see Hending, 2021), and the population density of *C. medius* in SIRNP may be limited by the ongoing forest degradation that is typical of the region (Seiler *et al.*, 2010); this also may explain the differences in density between Anabohazo (a continuous forest) and Ankarafa (a highly-degraded and fragmented forest). Furthermore, *C. medius* lives sympatrically with the northern giant mouse lemur (*Mirza zaza*), the Sambirano mouse lemur (*Microcebus sambiranensis*), and the Sahamalaza sportive lemur (*Lepilemur sahamalaza*) in SIRNP (Hending *et al.*, 2017c, 2022a). Although niche separation exists between these species, all four of these taxa require secure sleeping sites. Well-insulated tree holes are particularly sought after by these species, because they provide cover from predators and insulation from the cold (Hending *et al.*, 2017c; Rode *et al.*, 2013; Schmid, 1998; Seiler *et al.*, 2013). Tree holes are particularly important for *C. medius*, and the high competition for these sleeping sites also may limit *C. medius* numbers in the forests of SIRNP, which has been observed in other cheirogaleid lemurs (Lutermann *et al.*, 2010).

Although all *Cheirogaleus* are obligate hibernators (Dausmann & Blanco, 2016), many surveys of their population structure and density have occurred partly or entirely in Madagascar's dry season, a period during which they are likely hibernating (Herrera *et al.*, 2011; Lehman *et al.*, 2006; Müller, 1998; Müller *et al.*, 2000). We found significant differences in our encounter rate of *C. medius* between the wet and dry seasons. From these findings, it is clear that results of surveys that included either wholly or partly the hibernation period do not represent accurate population density values and are serious underestimates of total population size. Such underestimates would be detrimental for accurate IUCN Red List assessments for *Cheirogaleus*, considering that their forest habitat is highly threatened by deforestation and unmitigated climate change (Hending *et al.*, 2022b; Vieilledent *et al.*, 2018). Our results underpin the importance of a sound understanding of the activity periods of *Cheirogaleus* populations at specific sites and in specific habitats so that population surveys can be carried out at the correct time to calculate accurate and reliable population assessments.

Summary and Future Directions

This study provides an overview of seasonal activity level, hibernation and population density of *C. medius* in a transitional forest habitat. However, we still know nothing of the behavioural ecology of this species in transitional forest and how it compares to that of the *C. medius* populations in dry forest. To better understand *C. medius* ecology and hibernation and how it varies among habitat types and

bioclimatic regions, the thermoregulatory physiology and hibernaculum choice of *C. medius* should be investigated for the populations in SIRNP, because these determine *Cheirogaleus* ecology and hibernation expression (Dausmann & Blanco, 2016). Furthermore, a more detailed knowledge of *C. medius* feeding ecology is needed and its implications for hyperphagy (the prehibernation “fattening” period) need to be explored (Fietz & Ganzhorn, 1999). Generally, the ecology and natural history of *C. medius* is still little known despite the large geographic distribution of this species. Such datasets may provide answers as to how and why lemurs have evolved a survival strategy as extreme as obligatory hibernation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10764-023-00353-y>.

Acknowledgements The authors thank the field guides, Raumiald, Mahatsara, Avitsara, Hervé, Aristide, and Jacquis, and cooks, Klariny, Klarice, and Marceline, for all their help and enthusiasm during our time together in the field. We also express our sincere gratitude to the people of Ambinda, Betsimpoaka, Marovato, Maropapango, Antanandava, Antanambao Manambaro, Antafiabe, Maromandia, and Ambolobozo for their logistical assistance. We are grateful to MICET and MNP for their facilitation services and for kindly allowing us to conduct research within the Sahamalaza-Iles Radama National Park (permit numbers 245/19 and 124/22—MEEF/SG/DGGE/DAPRNE/SCBE.Re). We thank National Geographic Society, Global Wildlife Conservation, Primate Conservation Incorporated, La Vallée des Singes, Idea Wild, Primate Society of Great Britain, AEECL, the University of Bristol, and many private donors for kindly funding this fieldwork. Finally, thanks to the handling editor and two anonymous reviewers whose comments enabled us to improve the quality of this paper.

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