



Diel activity guild drives different mammal responses to fragmentation and degradation in the Amazon deforestation arc

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Abstract

Fragmentation and degradation have profound effects on species' habitat use and activity patterns. According to their diel activity guild, species may respond differently to environmental change, with diurnal species expected to be more vulnerable to these changes. Here, we test this hypothesis by investigating how fragmentation, and degradation modulate the habitat use and overlap in diel activity of contrasting mammal diel activity guilds in the Amazonian arc of deforestation. We used data from camera-traps (2,970 trap-days) across 30 forest fragments (from 8 to 435 ha) and three continuous forest sites. Considering diurnal and nocturnal mammals separately, we examine (1) the effects of fragmentation, and degradation on the habitat use and (2) the overlap in their diel activity across the different forest sizes. Habitat use by diurnal mammals increased with forest size, but not that of nocturnal species. In general, diurnal mammals anticipate their peak activity from 00:00 h to 6:00 h into smaller fragments (<100 ha). The diel activity patterns of diurnal mammals in small (<50 ha) and large (<500 ha) fragments were diverged to those in continuous forest. On the other hand, the diel activity patterns of nocturnal mammals across all size categories showed high overlap with those in continuous forest, indicating that diel activity patterns remained constant along the forest-size gradient. Such behavioral responses of diurnal mammals may be due to changes in fragment size, which alter the temporal availability of trophic resources and, consequently, may increase interspecific competition for limited resources. These findings comprise baseline knowledge informing evidence-based mechanisms of mammalian adaptation in human-modified regions across the tropics.

Keywords Activity patterns · Tropical forest · Forest size · Mammals · Rondônia endemism zone

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Introduction

Human activities exert profound negative impacts on the biosphere, with approximately 75% of terrestrial areas under human-induced pressures such as overexploitation and land-cover change (Venter et al. 2016). These pressures have placed around 46,300 species at risk of extinction (IUCN 2024). Among the main factors causing biodiversity loss, habitat loss and fragmentation stand out as critical threats (Püttker et al. 2020), given that, at the patch scale, these changes act synergistically (i.e., decrease size and increase isolation; Riva and Fahrig 2023; Fletcher Jr. et al. 2023; Goebel et al. 2025a). For example, the conversion of Amazonian forests—mainly for agriculture and pasture—has resulted in landscapes dominated by habitat fragments of varying sizes and degrees of isolation embedded within an anthropogenic matrix (Fearnside et al. 2005; Goebel et al. 2025a). These changes also create edge effects (Louthan et al. 2015), that alter vegetation structure and restrict trophic and structural resources (Harper et al. 2005). Habitat degradation is further exacerbated by additional human activities, including fires, livestock farming, and logging (Benchimol and Peres 2015; Barlow et al. 2016), which further simplify habitat structure.

Despite widespread evidence on the negative impacts on biodiversity from habitat loss, fragmentation, and consequent degradation across the tropics (Haddad et al. 2015), less is known about species behavioral responses. In the aftermath of the fragmentation process, persisting species might change the intensity with which they use the habitat, as well as their diel activity patterns (Tuomainen et al. 2011; Norris et al. 2010; Mendes et al. 2020). A recent meta-analysis revealed that the effects of human disturbance are more drastic for diurnal species (Gaynor et al. 2018), which tend to use less intensively human-disturbed habitats (Palmeirim et al. 2025) and may become more nocturnal to avoid contact with humans and minimize the risk of predation (Ordiz et al. 2017). In fragmented landscapes, an increase in nocturnal activities by diurnal species has been reported for the collared peccary (*Dicotyles tajacu*) and the agouti (*Dasyprocta* sp.) (Norris et al. 2010; Mendes et al. 2020).

In fragmented landscapes, species habitat uses and diel activity patterns may vary according to the environmental characteristics, including size, isolation, and habitat alterations (Norris et al. 2010; Palmeirim et al. 2025). For instance, diurnal species persisting in smaller, more isolated forest fragments are further subject to more prominent edge effects (Norris et al. 2010). Smaller fragments present simplified habitats, with greater canopy openness and lower height, that alter microclimatic conditions due to the increased light penetration (Laurance et al. 2018). Consequently, the climate may include higher temperatures and lower humidity, and human use may be increased, especially during the day, which is expected to affect mammal activity patterns. Additional factors that may affect diel activity patterns in disturbed habitats include higher intra- and interspecific competition (Cunningham et al. 2019), resource availability (Foster et al. 2013), human lighting (Hoffmann et al. 2018; Mendes et al. 2020), and the presence of the domestic species (Gálvez et al. 2021). Such changes can be assessed by considering the overlap in species diel activity (Araújo-Fernandes et al. 2025; Palmeirim et al. 2025). Species diel activity is expected to contrast the most between the highest contrast between environmental conditions imposed by the degree of habitat fragmentation and degradation, for which the diel activity overlap would be lower.

Changes in temporal activity patterns can result in diverse consequences, such as excessive energy expenditure, which can reduce individual fitness (Kronfeld-Schor and Dayan

2003; Hut et al. 2012). Furthermore, it can trigger population declines or local extinctions, cascading effects, and significant changes in the food web, affecting essential ecological functions, like predation and seed dispersal (Gálvez et al. 2021; Carreira et al. 2020). Additionally, these behavioral changes can influence population persistence by increasing interspecific competition and niche overlap (Smith et al. 2018; Gaynor et al. 2018). Therefore, understanding changes in multispecies circadian activities offers valuable insights for ecology and conservation (Frey et al. 2017) by revealing how species adjust their activity patterns in response to habitat alteration and human disturbance, especially in biodiverse regions under high anthropogenic pressure, such as the southern Amazon.

Here, we aimed to investigate the effects of fragmentation and consequent degradation on habitat use and diel activity patterns of two contrasting diel activity mammal guilds—diurnal and nocturnal species—in an Amazonian arc of deforestation. We surveyed mammals using camera traps across 30 forest fragments and 3 sites in a continuous forest within a vast fragmented landscape (~7,900 km²) in southwestern Amazonia, Brazil. We hypothesize that (1) habitat use by mammals, particularly diurnal species, is lower in smaller, isolated and habitat-degraded fragments, and that (2) the diel activity patterns of mammals increasingly differ according to the differences in forest area, so that diel activity overlap is expected to be lower between smaller fragments (< 50 ha) and continuous forests, and higher between larger fragments (> 100 ha) and continuous forests.

Methods

Study area

Our study was conducted in southwestern Amazonia, Brazil, in a highly fragmented landscape across the “Arc of Deforestation” (Fig. 1). The study sites are in the municipalities of Ji-Paraná, Jaru, Ouro Preto D’Oeste, Vale do Paraíso, and Theobroma, covering an area of ~7,900 km², in the state of Rondônia. The study region comprises an endemism center of the Amazon basin (i.e., the Rondônia endemism zone in the Rondônia biogeographic province) and harbour a rich diversity of mammal species (322 species: Marsh et al. 2022, including 29 primates: Oliveira et al. 2024). This ecoregion of the Open Ombrophilous Amazon Forest (Brazil 2010) is currently characterized by the presence of several fragments with different sizes, shapes, and degrees of isolation (Goebel et al., 2025a), embedded within a matrix predominantly composed of cattle pasture and, to a lesser extent, by plantations with alternating cultivation of soybeans and corn. In this landscape, the Jaru Biological Reserve (REBIO Jaru) and the Igarapé Lourdes Indigenous Land represent the largest remaining forests, totalling 540,753 hectares interconnected (Goebel et al. 2025a; 2025b). The predominant climate is Tropical Rainforest, characterized by an annual precipitation of ~2,000 mm and an average annual temperature of 26 °C, with two well-defined seasons: a dry season from May to October and a rainy season from November to April (Alvares et al. 2013).

We conducted our research in 30 forest fragments located in private areas and along three widely spaced neighbouring sites in the continuous forest sites (CFs) across the protected area of Jaru Biological Reserve (REBIO Jaru), totalling 33 independent sampling sites. We selected fragment sites spaced at least 5 km apart to improve sample independence. The

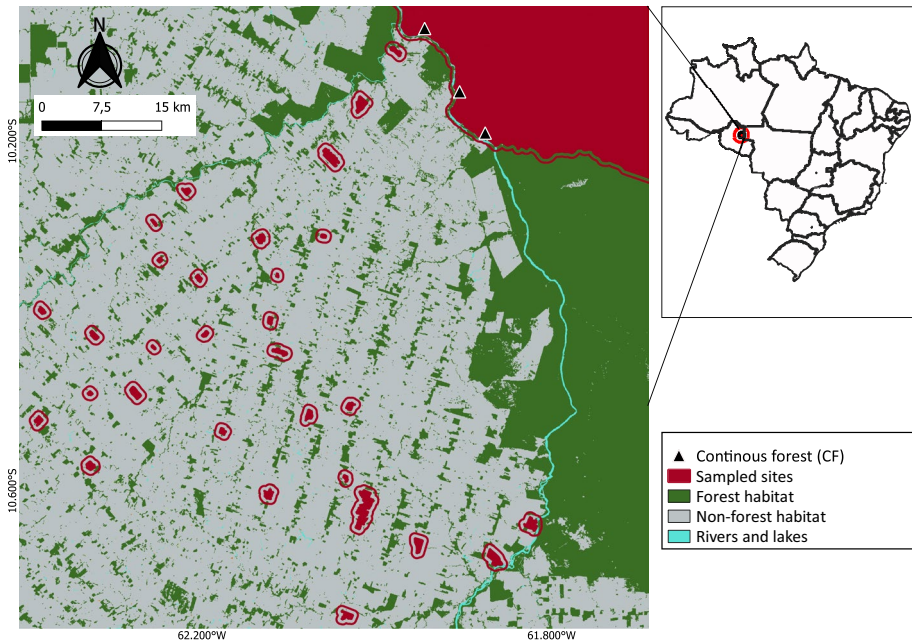


Fig. 1 Distribution of surveyed sites in a fragmented landscape in the arc of deforestation, Brazilian Amazon. The 30 forest fragments are highlighted in red, and three continuous forest sites (REBIO Jaru) are shown with black triangles with white borders (CF1, CF2, and CF3) in the Jaru Biological Reserve (REBIO Jaru), a protected area in Rondônia state

fragments surveyed ranged from 8.0 ha to 435 ha (Table S1; S2), while the continuous forest — REBIO Jaru — has 343,000 ha.

Mammal surveys

Mammal communities were sampled between February 2022 and May 2023, with three fragments being sampled per month. We installed three camera-traps (hereinafter CTs; Bushnell® 119932C and Browning® BT6) at each study site and baited them with salt to increase species detection rates (Duarte et al. 2018). To reduce potential bias introduced by baiting, each CT received a standardized amount of salt (1 kg), consistently placed at the center of the detection field at the time of deployment. CTs were deployed ~50 cm above the ground and spaced at least 500 m apart (Benchimol and Peres 2015), except for nine fragments smaller than 50 hectares and with irregular shapes, which required the shortest distance (200 m) between the CTs (Goebel et al. 2025b). To reduce potential edge effects, CTs were preferentially placed in the forest core, and, in smaller fragments, due to area limitations, they were positioned at least 150 m from the nearest forest edge. CTs were configured to record 10-s videos with a 5-s interval between recordings. CTs operated 24 h a day, for 30 consecutive days, totalling 2,970 camera-trap days of sampling effort. In consecutive records of the same species at the same station, we considered a 30-min interval to define an independent detection (Norris et al. 2010; Benchimol et al. 2015).

Each mammal species was identified to the species or genus level by analysing morphological characters based on an identification guide (Borges et al. 2004). The taxonomic classification of mammal species followed Abreu-Jr et al. (2024). Although we were able to identify most species, records of *Coendou* sp., *Proechimys* sp., *Dasyprocta* sp., *Hylaeamys* sp., and *Marmosa* sp. were considered at the genus level. For simplicity, we refer to taxa identified at both the species and genus levels as “species”. In the analysis of diel activity patterns, we excluded arboreal species because they are lowly detectable with CTs at floor level (Carreira et al. 2020). We classified each species as either diurnal or nocturnal, based on its predominant activity period as described in the literature (Wilman et al. 2014; Magioli et al. 2015; see Table S3).

Habitat variables

Land use and land cover data were obtained using satellite images from 2021 (MapBiomass 2021) provided by the MapBiomass project (<https://brasil.mapbiomas.org/>, collection 7.1), matching the timing of the mammal surveys. We measured the forest size of each sampling site (*forest size*) by creating shapefiles in the QGIS 3.22 LTR software (QGIS Development Team 2023). Subsequently, we divided the 33 forest fragments into four categories: small (≤ 50 ha), midsized (> 50 to ≤ 100 ha), large fragments (> 100 ha to 500 ha), and CFs (i.e., the sampling sites within the REBIO Jaru, comprising the largest CFs in the region) (Table S1). We calculated the minimum linear distances between the largest remnant of the region (i.e., REBIO Jaru and Indigenous Land Igarapé Lourdes) and the edge of any sampling sites (*distance*) using R code, based on site coordinates expressed in latlong (DATUM SIRGAS 2000). To quantify the mean vegetation height (m) for each site, we used rasterized data obtained from Potapov et al. (2021; available at <https://glad.umd.edu/dataset/gedi>). To quantify the number of cut trees, we used one linear transect per fragment, originally established for biodiversity sampling (see Goebel et al. 2025b), with lengths ranging from 1.0 to 3.0 km. Each transect was traversed once to quantify the number of cut trees (*cut trees*) in a 10-m strip on each side of the transect. For each fragment, we classified sampling events according to the season (*season*) in which they occurred, defining a dry season from May to October and a rainy season from November to April (Alvares et al. 2013). We used the perimeter-to-area ratio (*patch shape*) as a proxy for edge-effect intensity (e.g., Benchimol and Peres 2015; Palmeirim et al. 2020), with higher values indicating a greater proportion of edge relative to patch area.

Data analysis

Habitat use

We performed a Pearson correlation matrix to control for additional high levels of variable interdependence ($r > 0.75$). This prior selection included the forest size and cut trees. The distance ($r = 0.83$) and mean vegetation height ($r = 0.79$) were excluded due to high correlation with forest size. Then, we verified whether habitat use by diurnal or nocturnal species (given by $\log x + 1$ -transformed number of independent records per site) was affected by forest size, the number of cut trees, and patch shape. To do this, we performed Generalized Linear Mixed Models (GLMMs) with a negative binomial distribution and using season as a

random variable. The GLMM was specified as follows: number of records ~ forest size + cut trees + patch shape + offset (active camera-trap days) + (1|season).

For the habitat use of diurnal species, the marginal R^2 (R^2_m) and conditional R^2 (R^2_c) were 0.15. For nocturnal species, the marginal and conditional R^2 were 0.003 ($R^2_m=0.003$, $R^2_c=0.003$). We therefore removed the random variable from subsequent analysis, thereby applying Generalised Linear Models (GLMs).

Separate models were fitted for diurnal and nocturnal records with a negative binomial distribution to account for overdispersion. Model residuals were then examined using the dharma R package (Hartig 2022), with no issues being reported. A candidate model set was further constructed, using all combinations of the explanatory variables retained (including the null model restricted only to the intercept and residual variance). Models were ranked based on their AIC values corrected for small sample sizes (AICc: Burnham and Anderson 2002), using the MuMIn R package (Bartoń 2016). To account for model uncertainty in multi-model inference, a model-averaging approach was performed whenever multiple plausible models (i.e., $AIC > 2$) were obtained (Table S5). Prior to model averaging, explanatory variables were standardized ($\bar{x} = 0$, $\sigma = 1$) to place coefficient estimates onto the same scale.

Diel activity patterns and overlap

Our approach focused on analyzing the univariate influence of patch size on species behaviour. For the interpretation of the results, we defined the nocturnal period between 18:01—05:59 h and the diurnal period between 06:00—18:00 h (Carreira et al. 2020; Table S4). First, we converted time to a radian scale, ranging from zero hours (0) to 24 h (2π). We calculated overlap coefficients to quantify similarities in mammal activity patterns between the CFs and each forest fragment category (small, midsized, and large). This analysis was conducted separately for diurnal and nocturnal species to account for their distinct activity patterns. The overlap coefficients (Δ) range from 0 (no overlap) to 1 (complete overlap) and quantify the degree of similarity in activity patterns between species guilds (i.e., nocturnal and diurnal species), or across forest size categories. These metrics were calculated using the ‘overlap’ R package (Meredith et al. 2014). We followed the established recommendations of Ridout and Linkie (2009) and Araújo-Fernandes et al. (2025) and chose to use the overlap estimator “Dhat4” (Δ_4), which performs more consistently in larger samples exceeding 50 observations.

Furthermore, the two most frequently detected species (i.e., those with more than 25 detections per forest size category) were analysed separately. For *Proechimys* sp., we calculated overlap coefficients to quantify similarities in activity patterns between large forest fragments and small and midsized fragments. The CFs were excluded from this analysis due to the low number of records. We used the overlap estimator (Δ_1). For *Dasyprocta* sp., we calculated overlap coefficients to quantify similarities in mammal activity patterns between the CFs and each forest fragment category (small, midsized, and large), using the estimator Dhat1. To assess whether the data sets under comparison originated from identical distributions, we performed a probability test using the “compareCkern” function in the ‘activity’ R package (Rowcliffe et al. 2014). This function tested whether the species activity distributions for each guild varied between one of the fragment size categories and those in the CFs sites. We considered the overlap in diel activity between one of the fragment size cat-

egories and CFs sites to be lower than expected by chance for $p < 0.05$ (Rivero-Monteagudo and Mena 2023; Araújo-Fernandes et al. 2025). Following the methodology of Ridout and Linkie (2009), we estimated confidence intervals with 95% certainty (CI 95%), using a bootstrap technique with 9,999 resamples.

For data visualization, we first employed a kernel density function and calculated the overlap coefficient. We used a smoothing parameter ($k_{max}=3$) for kernel density estimation, which provides robust estimates across unimodal and bimodal activity distributions (Ridout and Linkie 2009; Rivero-Monteagudo and Mena 2023). Additionally, we applied a bandwidth adjustment factor of one to fine-tune density estimation and improve the visualization of activity patterns. Proper selection of k_{max} and adjustment values is crucial to avoid over-smoothing and introduce noise (Rivero-Monteagudo and Mena 2023). These parameters enabled the use of the Dhat4 estimator for subsequent analysis, considering the recording times as part of a continuous circular distribution (Lashley et al. 2018).

Results

We obtained 1,758 independent mammal records across 30 forest fragments and 3 CFs (Table S4). Among the 31 species recorded, 20 (62.5% of the records) were classified as nocturnal and 11 (37.5%) as diurnal (Table S3). We detected 21 species in small fragments, 20 in mid-sized fragments, 22 in large fragments, and 16 in CFs. Among nocturnal species, the most frequent were *Proechimys* sp. (46%), *Dasybus novemcinctus* (18%), and *Cuniculus paca* (15%; Fig. 3). The most frequently recorded diurnal species were *Dasyprocta* sp. (34%), *Dicotyles tajacu* (15%), and *Tamandua tetradactyla* (14%). The activity at both species and guild levels varied across forest size categories (Fig. 3). In the fragmented areas, nocturnal activity was more predominant (Fig. 2A, B and C), while in CFs, the activity of diurnal species was more pronounced (2D).

Habitat use

In small fragments (Fig. 2A), 74% of the records corresponded to nocturnal mammals and 26% to diurnal species. In mid-sized (Fig. 2B) and large fragments (Fig. 2C), nocturnal mammals were also predominant, accounting for 63% of the records in both cases, while diurnal species represented 37%. In contrast, in the CFs (Fig. 2D), 58% of the records were from diurnal mammals and 42% of nocturnal species (Fig. 2). Forest size, number of cut trees, and patch shape were retained as explanatory variables, while isolation distance and mean vegetation height were excluded due to high interdependence. Habitat use was best explained by the model including only forest size ($AICc=260.1$; $\Delta AICc=0$; $w=0.34$; Table S5). Habitat use by diurnal mammals increased with forest size (z -value=2.14, $p=0.03$; Fig. 3B). However, habitat use by nocturnal mammals remained unaffected by any of the variables considered (Table S6; Fig. 3A).

Diel activity patterns and overlap

Diel activity patterns varied between forest fragments and CFs sites, resulting in distinct diel activity among forest fragments for both nocturnal and diurnal species (Fig. 4). For noctur-

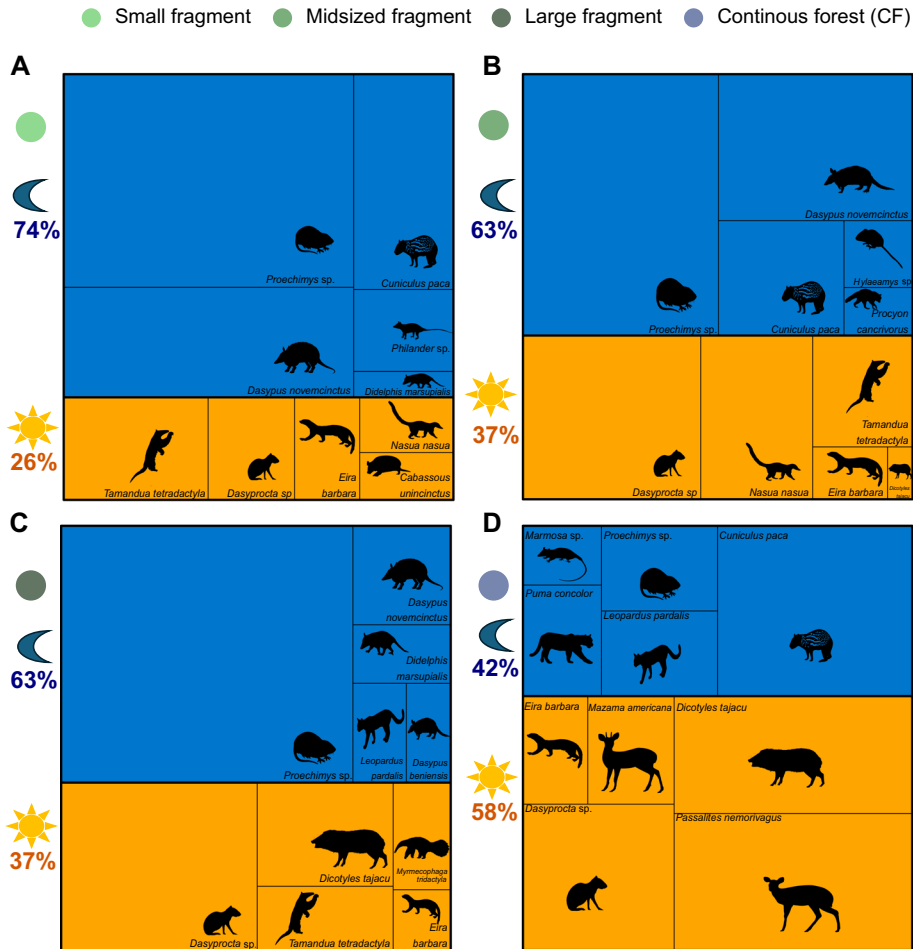


Fig. 2 Number of records per species per category of forest size: (a) small fragments, (b) midsized, (c) large, and (d) continuous forest. In every panel, each rectangle represents a species and is sized according to the proportion of records for the corresponding species. Rectangles are color-coded according to the diel activity guild of each species: nocturnal (blue) and diurnal (orange). The values provided at the top correspond to the proportion of records for each diel activity guild per forest size category. Only the five most recorded species per diel activity guild (diurnal and nocturnal) were included in each forest size category

nal species, the overlap with the CFs was similar across all three fragment sizes (Fig. 4A). In smaller fragments, the activity of nocturnal species peaks in the early evening (~18:00 h) and gradually decreases in the early morning (~5:00 h; Fig. 4A). In midsized fragments (Fig. 4B), nocturnal mammals showed three distinct activity peaks (~21:00 h, ~00:00 h, and ~05:00 h). In large fragments, mammals displayed two peaks (~19:00 h and ~02:00 h; Fig. 4C). Overall, nocturnal mammal activity in the CFs started earlier (~05:00 h) than in the forest fragments and exhibited a single main peak (~00:00 h; Fig. 4).

For diurnal species, activity in small fragments was characterized by two peaks, one in the afternoon (~17:00 h) and one in the evening (~03:00 h; Fig. 4D). However, in the

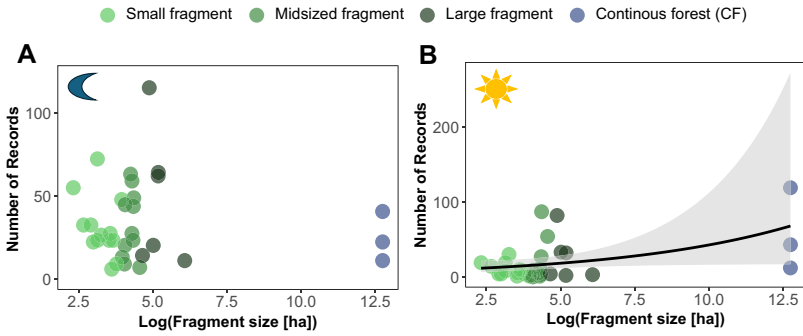


Fig. 3 Relationships between environmental variables and the intensity of species habitat use (number of mammal records) in the Amazon deforestation arc, where: **(a)** the relationship between habitat use (number of records) of nocturnal mammals and forest size; **(b)** between habitat use of diurnal mammals and forest size. Lines are the model adjusted for the stronger relationships ($P \leq 0.05$), and shaded areas represent the 95% confidence region

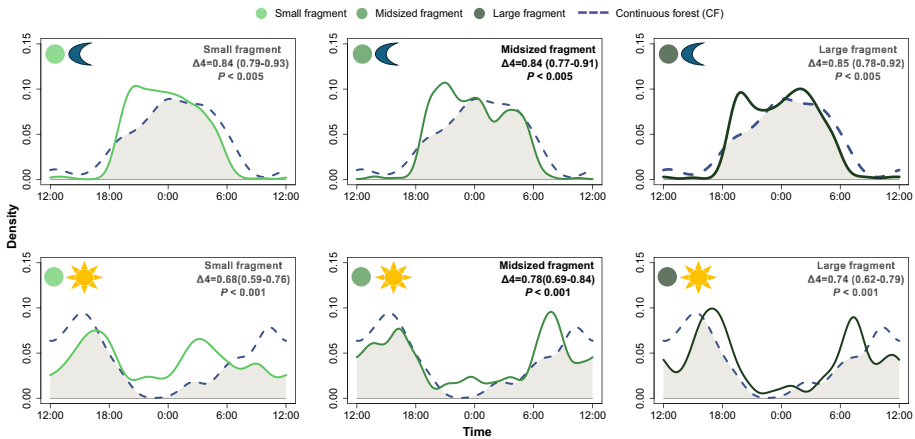


Fig. 4 Diel activity patterns of nocturnal and diurnal mammals in 33 fragments of different habitat sizes in a highly fragmented landscape across the arc of deforestation, in Rondônia state, Brazil. The comparison of the activity patterns of continuous forest for nocturnal mammals (**a–c**) and diurnal mammals (**d–f**) was conducted in small (< 50 ha), midsized (> 50 to < 100 ha), and large fragments (> 100 to 500 ha) with continuous areas. Blue lines indicate the activity for the continuous area. The green lines indicate the fragments, with colour intensity increasing with fragment size

CFs, activity peaked from early afternoon (~ 15:00 h) until dusk and again in the morning (~ 10:00 h). Activity of diurnal species in midsized fragments also exhibited two peaks: one in the early afternoon (~ 12:00–18:00 h) and another during the morning (~ 06:00–10:00 h; Fig. 4E). For large fragments, there was a higher peak of activity in the morning (~ 07:00 h) and early afternoon (~ 17:00 h; Fig. 4F). Given the forest size categories, diurnal mammal activity between small fragments and CFs showed an overlap coefficient of 0.68 (CI 95% [0.59–0.76], $p < 0.001$). In contrast, activity between midsized and CFs exhibited an overlap coefficient of 0.78 (CI [0.69–0.84], $p < 0.001$; Fig. 4E). When excluding records of *Pro-*

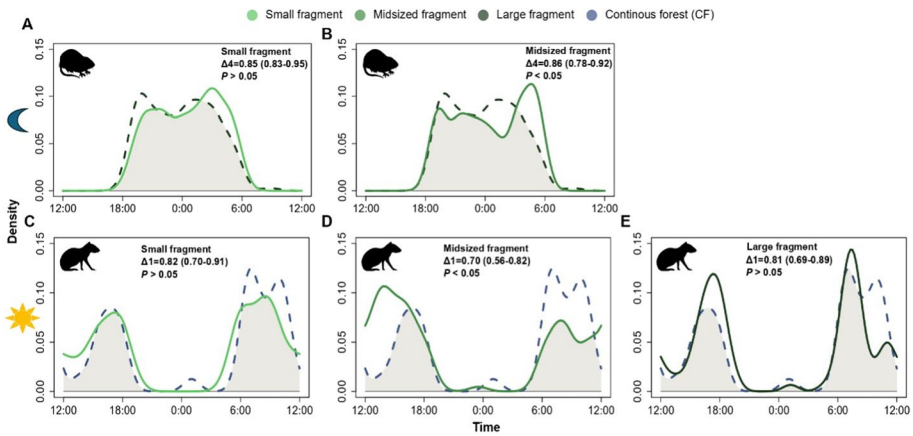


Fig. 5 Comparison of the diel activity patterns for each most frequently recorded species (i.e., those with more than 25 detections by forest size categories): (a–b) the nocturnal *Proechimys* sp., and (c–e) the diurnal *Dasyprocta* sp. in fragments in the Amazon. For each comparison, the overlap coefficient, its confidence intervals, and the P -value (testing whether the probability that the two distributions derive from the same distribution). Overlay analyses for *Proechimys* sp. were conducted by comparing the large fragments with other fragments. For *Dasyprocta* sp., comparisons were conducted between the CFs and fragments of different size classes. The green lines indicate the fragments, with colour intensity increasing with fragment size. Blue lines indicate the activity for the continuous area

echimys sp. (510 records) and *Dasyprocta* sp. (226 records), a similar pattern was observed (Figure S1).

The specific activity patterns of each species varied among forest size categories (Fig. 5). For the nocturnal species *Proechimys* sp., the activity pattern differed between large and mid-sized fragments ($\Delta 4 = 0.86$; CI 95% [0.78–0.92], $p < 0.05$). Activity peaks occur around 10:00 h and 4:00 h (Fig. 5). Considering forest size categories, the diurnal species *Dasyprocta* sp. showed the lowest coefficient of overlap than expected by chance in diurnal mammal activity between mid-sized fragments and the CFs ($\Delta 1 = 0.70$; CI 95% [0.56–0.82], $p < 0.05$). The overlap in diurnal activity between large and small fragments was 0.82 (0.70–0.91) and 0.81 (0.69–0.89) between large and mid-sized fragments. In the CFs, small- and large-sized fragments, the activity peaks of *Dasyprocta* sp. occurred around 08:00 h and 16:00 h (Fig. 5D and F). In mid-sized fragments, a peak was observed at 14:00 h and 08:00 h (Fig. 5E).

Discussion

Fragmentation, habitat loss, and degradation have been proven to be a critical determinant of overall mammal diversity in tropical fragmented landscapes, including in the Amazon biome (Benchimol and Peres 2015; Palmeirim et al. 2020). However, the mechanisms of behavior adopted by species as a function of environmental conditions remain unknown. Here, we expand the discussion on how habitat fragmentation and degradation affect biodiversity by further driving mammal habitat use and diel activity patterns. Habitat use by diurnal mammals decreased in small fragments, while the number of cut trees and patch shape did not significantly affect use by diurnal and nocturnal mammals. Furthermore, we

observed differences in the temporal overlap coefficients between the fragments and the CFs, which reflect changes in mammals' activity peaks, especially diurnal ones. Our results suggest that diurnal mammals have increased their nocturnal activity in small fragments, and their diel activity patterns are more similar between mid-sized fragments and CFs. In contrast, for nocturnal mammals, activity patterns between fragments and CFs are similar.

Indeed, in a previous study using the same dataset, we observed that, at the habitat scale, fragment size and height of vegetation affect the richness and ecological requirements of mammals (Goebel et al. 2025b). Additionally, our study reveals that forest size affects habitat use only by diurnal mammals, while logging intensity (i.e., cut trees) and patch shape had no significant effect on habitat use by the species analyzed. This result was expected, as larger forest areas and CFs offer more favorable environmental conditions, such as a greater diversity of trophic resources, roosts, and microclimates, allowing the co-occurrence of species with different ecological niches (Palmeirim et al. 2020; Goebel et al. 2025b) and mammal activity (Laurance et al. 2018). Similar results were found by Norris et al. (2010) in a study conducted in the Amazon, where logging intensity also did not influence mammal activity. For diurnal mammals, the effect may be more drastic, as the fragments are subject to some degree of daytime use (e.g., livestock management, use of nearby roads), which may lead these species to avoid times with greater anthropogenic disturbance (Mendes et al. 2020). Considering the patterns revealed by the species, our results showed that in forest fragments, smaller and nocturnal species are more frequent (e.g., *Proechimys* sp.). According to Galetti et al. (2015), areas where large mammals are eliminated result in a greater dominance of generalist rodents (e.g., *Proechimys* sp.), seed predators, and meso-predators (Pires and Galetti 2023). In CFs, medium- to large-sized mammals were more frequent (e.g., *Mazama americana*, *Puma concolor*), whereas habitat use between diurnal and nocturnal species is more balanced, which may reduce direct competition for resources such as trophic and spatial resources (Bennie et al. 2014). In general, changes in habitat use patterns can reflect behavioral adaptations in fragmented landscapes.

In terms of the diel activity patterns, we observed that activity overlap with CFs was similar across all three fragment sizes for nocturnal mammals. Nocturnal species showed peak activity between 18:00 and 22:00 h in forest fragments, whereas in CFs the peak occurred between 22:00 and 06:00 h. However, diurnal mammals showed greater variation in overlap coefficients between forest size categories. For example, in small fragments, peak activity occurs at 03:00 h and 17:00 h, while in CFs it occurs at 10:00 h and 15:00 h. The two peaks observed in small fragments may indicate habitat changes and a tendency towards "nocturnalization" (i.e., increased activity at night), possibly in response to increased human disturbance and increased vulnerability in degraded habitats (Gaynor et al. 2018; Mendes et al. 2020). With the reduction in forest height and vegetation cover described for small fragments, it may reflect the penetration of more sunlight (Harper et al. 2005) and bring the nightfall forward. Furthermore, the activity peaks of diurnal mammals are more restricted to dusk, and dawn may be related to the avoidance of times with higher temperatures (Peterson et al. 2021). According to the results obtained by Gaynor et al. (2018), although many species increased their nocturnal activity to avoid humans, those that were already nocturnal showed minimal changes in their activity time, indicating they can maintain natural behavior without significant temporal adjustments (Procko et al. 2023). Mammals, such as collared peccary (*Dicotyles tajacu*), white-lipped peccary (*Tayassu pecari*), ocelot (*Leopardus pardalis*), and nine-banded armadillo (*Dasypus novemcinctus*), are examples of species that

tend to become more nocturnal to persist in modified habitats (Norris et al. 2017; Mendes et al. 2020). In midsized and large fragments, activity patterns were more similar to those observed in the CFs, indicating that increasing fragment size may attenuate the effects of fragmentation on the temporal ecology of diurnal mammals.

The spiny rat (*Proechimys* sp.) was strictly nocturnal, corroborating Emmons (1997) and Silva et al. (2014). We would expect a greater difference in activity patterns between small and large fragments; however, the most distinct patterns are observed between midsized and large fragments. For the diurnal species agouti (*Dasyprocta* sp.), the most distinct patterns are observed between midsized and CFs. Overall, the agouti was strictly diurnal, with activity peaking in the early morning and afternoon, still, in midsized fragments, there was an advance of the afternoon peak and a delay in late-afternoon activity. Changes in diel activity patterns, like lower activity during daytime, that altered foraging patterns and interspecific competition, may have implications for the survival of mammals in altered landscapes (Gaynor et al. 2018). For instance, these changes may have effects on animal physiology and fitness, affecting demography, triggering trophic cascades (Gaynor et al. 2018), and harming essential ecological functions such as seed dispersal and population control (Gálvez et al. 2021; Carreira et al. 2020).

Following a previous study that revealed drastic declines in biodiversity (Goebel et al. 2025b), our results represent an advance in understanding species' behavioral responses to land-use changes in the Amazon deforestation arc. Although the use of baits can theoretically induce biases by altering natural activity patterns, as discussed by Rowcliffe et al. (2014), the controlled and standardized application of this methodology can significantly reduce these impacts, allowing for a reliable comparison between different fragments. In hard-to-reach areas, like the Amazon, where time and financial resources are limited and elusive species occur, the use of bait proves to be a valuable tool to increase the detection rate (Duarte et al. 2018) and provide crucial data on mammal activity. Previous studies, such as those by Meek et al. (2012) and Caravaggi et al. (2018), also used baits to attract animals and assess their activity periods. However, a caveat to our results is imposed by the sampling effort of nights (30 days per site), which did not allow us to undertake a species-specific analysis due to the limited number of records for each species for all forest size categories (i.e., less than 25 records per species by species in each forest size category). As with species-level effects, where behavioral plasticity is an important determinant of species persistence (Norris et al. 2010; Mendes et al. 2020), we recommend that future studies consider species-level responses, as well as seasonality.

We acknowledge that our analyses do not explicitly account for potential variation in species composition among fragments. Consequently, observed differences in activity overlap may partly reflect compositional turnover or shifts in community body-size structure, rather than purely behavioral responses. Given the documented decline in shared diversity along gradients of habitat loss and fragmentation in the region (see Goebel et al. 2025a, b), aggregating detections within fragment size categories may partially reduce compositional heterogeneity among fragments. Despite that, this assumption remains untested and should be considered when interpreting guild-level behavioral patterns. Yet, considering this limitation, our results demonstrate the ability of species to adjust their habitat use and activity patterns in response to changes in forest size in an important zone of endemism located in the arc of deforestation. Forest fragmentation has significantly altered mammal habitat use, favoring greater nocturnal activity in forest fragments, while continuous forest has more

balanced habitat use rates between diurnal and nocturnal species. The adaptability of mammals in this portion of the Amazon is mediated by their ability to adjust their diel activity patterns to persist along the fragment size gradient, especially in smaller fragments, which are more vulnerable to further fragmentation and habitat degradation (Norris et al. 2010). Therefore, our findings highlight the importance of preserving larger forest areas, including large fragments (> 100 ha), since they favour maintenance of diurnal mammals' activity patterns closer to those observed in continuous forests. Furthermore, they help mitigate the impacts of fragmentation, especially for species with diurnal habits, which appear to be more vulnerable to changes imposed by fragmented landscapes. Conservation strategies should consider increasing the structure and integrity of habitats that support nocturnal and diurnal species to ensure ecosystem balance and biodiversity, such as increasing the size of fragments and avoiding degradation.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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