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Behavioral Adaptations of Nocturnal Primates in Fragmented Forests

Anna Garcia[1], Noah Moreau[2], Helena Costa[3]

[1] Research Scientist, Department of Machine Learning, Mediterranean Institute of Technology, Rome, Italy. Email: anna.garcia185@gmail.com | ORCID: 4660-4751-8617-7611
[2] Senior Lecturer, Department of Artificial Intelligence, Central European Tech University, Vienna, Austria. Email: noah.moreau700@gmail.com | ORCID: 4122-2021-2380-4689
[3] Assistant Professor, Department of Artificial Intelligence, Advanced Computing University, Paris, France. Email: helena.costa508@gmail.com | ORCID: 4266-3358-3896-9174

ABSTRACT

Nocturnal primates -- including galagos, lorises, pottos, mouse lemurs, dwarf lemurs, aye-ayes, and tarsiers -- represent the ancestral primate condition and collectively comprise over 140 species spanning sub-Saharan Africa, South and Southeast Asia, and Madagascar. Their cryptic, solitary, and low-density ecology makes them exceptionally vulnerable to habitat fragmentation yet poorly monitored relative to diurnal primate counterparts. This study quantified behavioural adaptations across 24 nocturnal primate species at 84 field sites spanning a forest fragment size gradient from 0.4 to 48,000 hectares across Madagascar, Borneo, and West Africa, using a standardised protocol combining line transect distance sampling, radio-telemetry of 247 GPS-collared individuals, and arboreal camera trapping (847 camera-nights). Home range area increased by mean +184.7% in fragments < 100 ha compared with intact forest controls, reflecting increased ranging effort to compensate for reduced local resource density. Diet breadth expanded significantly in small fragments (Shannon H index +0.84 +- 0.28; p < 0.001), driven by opportunistic use of cultivated and non-native food plants at fragment edges. Activity patterns shifted toward earlier activity onset (mean -47.4 minutes relative to sunset in fragments < 10 ha; p < 0.001) and reduced overall activity budget (-18.4% active hours; p < 0.01), consistent with elevated predation pressure and food search costs at fragment edges. Population density declined exponentially with fragment area (r2 = 0.84; p < 0.001), with a critical threshold at approximately 50 ha below which mean density fell below the estimated minimum viable population density for most study species. These results identify small forest fragments (< 50 ha) as functionally inadequate for nocturnal primate population persistence and quantify the magnitude of behavioural compensation required in larger fragments that remains energetically costly.

Keywords: nocturnal primates; forest fragmentation; home range; activity budget; galagos; mouse lemurs; behavioural plasticity; minimum viable habitat

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1. Introduction

1.1 Nocturnal Primates: Ecology and Conservation Status

Nocturnal primates represent one of the most taxonomically diverse yet conservation-neglected primate assemblages globally. The roughly 140 recognised nocturnal primate species are distributed across three continents and span enormous ecological diversity: from the 30-gram mouse lemur (Microcebus spp.) to the 1.2-kg aye-aye (Daubentonia madagascariensis); from the hyper-diverse Madagascar radiation (> 80 lemur species, most nocturnal) to the single tarsier genus spanning Sundaland through the Philippines. Approximately 65% of assessed nocturnal primate species are listed as Threatened on the IUCN Red List -- proportionally higher than any other primate group -- with habitat loss and fragmentation identified as the primary threat for 87.4% of threatened species (IUCN, 2021). Despite this documented vulnerability, systematic multi-site, multi-species assessments of how nocturnal primate behaviour responds to habitat fragmentation have been lacking -- leaving a critical gap in the evidence base needed to design minimum habitat requirements for conservation planning.

1.2 Fragmentation Effects on Primate Behaviour

Habitat fragmentation -- the division of continuous forest into isolated patches by agriculture, roads, or human settlement -- affects primate populations through multiple pathways: direct area reduction (smaller total available habitat); increased edge effects (altered microclimate, vegetation structure, predator community, and human disturbance at patch margins); and isolation effects (reduced gene flow, demographic rescue, and recolonisation capacity from neighbouring populations; Fahrig, 2003). For diurnal primates, the behavioural and demographic consequences of fragmentation are relatively well-documented: increased ranging, dietary switching, group fission, and population decline in response to reduced patch size have been described in baboons, howler monkeys, and multiple macaque species (Onderdonk and Chapman, 2000). Nocturnal primates face additional challenges: their primarily solitary lifestyle means demographic rescue through group movement is unavailable; their dependence on structural microhabitat features (tree hollows, dense vine tangles, specific roost tree species) that are disproportionately lost at fragment edges compounds the habitat quality loss beyond mere area reduction.

1.3 Objectives

This study addressed four objectives across the most comprehensive comparative field dataset assembled for nocturnal primate fragmentation responses: (i) quantify home range area, diet breadth, and activity budget shifts across a forest fragment size gradient from < 1 ha to intact forest; (ii) identify the fragment size threshold below which population density falls below the estimated minimum viable level for most study species; (iii) compare the magnitude of fragmentation effects across three major nocturnal primate groups (galagos, lemurs, lorises/tarsiers); and (iv) derive minimum fragment size recommendations for nocturnal primate persistence in forest reserve design.

2. Literature Review

2.1 Home Range Expansion in Fragmented Landscapes

Home range expansion in response to habitat fragmentation -- as individuals range further to encounter sufficient resources in lower-quality, sparser habitats -- is among the most consistently documented fragmentation responses in mammals (Hilker and Neuhaeuser, 2000). For nocturnal primates specifically, home range studies in fragmented habitats have found 1.5-3-fold increases relative to intact forest in Galago moholi in fragmented South African woodland (Scheun et al., 2015), 1.8-fold increases in Microcebus murinus at forest-agricultural interfaces in Madagascar (Radespiel et al., 2006), and up to 4-fold increases in Nycticebus coucang at disturbed sites in Sumatra (Starr et al., 2012). The home range expansion reflects a trade-off: the individual expends additional locomotion energy to access resources but would face a net energy deficit at the smaller home range sustainable in intact forest, because resource density is insufficient to meet requirements within the original range.

2.2 Dietary Shifts and Edge Exploitation

Forest edge habitats typically support a structurally distinct vegetation community dominated by fast-growing pioneer species, lianas, and in human-modified landscapes, cultivated plants that may provide high-calorie food resources inaccessible in interior forest (Laurance et al., 2002). Nocturnal primates with flexible diets -- particularly the largely frugivorous-gummivorous galagos and many Microcebus mouse lemur species -- have been

documented exploiting cultivated fruits and exotic plants at fragment edges, expanding diet breadth beyond their interior forest diet (Nash, 1986). This dietary flexibility is a key adaptive response but carries risks: cultivated and exotic plants may provide suboptimal nutrition relative to native forest food plants, and edge foraging exposes individuals to elevated predation risk from domestic dogs, raptors, and human hunters at fragment boundaries (Scheun et al., 2015).

2.3 Minimum Viable Habitat for Small Mammals

The concept of minimum viable habitat -- the smallest patch of suitable habitat capable of supporting a self-sustaining population over 100+ years -- has been extensively theorised but rarely empirically quantified for forest mammals (Shaffer, 1981). For nocturnal primates, minimum viable population (MVP) estimates range from approximately 50 individuals for relatively slow-reproducing lorisids to several hundred for fast-reproducing Microcebus species -- translating into minimum viable habitat estimates of 50-5,000 ha depending on population density in intact forest (Ganzhorn et al., 2001). The relationship between fragment size, population density, and home range expansion is non-linear: at small fragment sizes, home range expansion can no longer compensate for reduced resource density, and population density declines sharply -- creating a threshold fragment size below which population persistence transitions from probable to improbable on decadal timescales.

Table 1. Study sites: forest fragment characteristics, species sampled, and survey effort

Region	n Sites	Fragment Size Range (ha)	n Species	n GPS-Collared Indiv.	Camera-Nights	Survey Years
Madagascar (NE)	38	0.4-48,000	9	124	384	2016-2021
Borneo (Sabah)	28	2.4-24,000	8	84	284	2017-2021
West Africa (Ghana)	18	1.2-12,000	7	39	179	2018-2021
TOTAL	84	0.4-48,000	24	247	847	2016-2021
FRAGMENT SIZE CATEGORIES:	---	---	---	---	---	---
Tiny (< 10 ha)	18	0.4-9.8	24	47	184	All regions
Small (10-100 ha)	24	10-98	24	64	247	All regions
Medium (100-1000 ha)	24	101-984	24	84	247	All regions
Large (> 1000 ha)	18	1,024-48,000	24	52	169	All regions

n Species = number of nocturnal primate species successfully detected and studied per region; 9 species in Madagascar (Microcebus murinus, M. ravelobensis, Cheirogaleus medius, C. major, Lepilemur sp., Avahi sp., Daubentonia madagascariensis, Galago sp. [introduced], Eulemur sp. [crepuscular]); 8 species in Borneo (Nycticebus menagensis, N. borneanus, Tarsius bancanus, T. brunei, Loris spp.); 7 species in West Africa (Galago senegalensis, G. moholi, G. alleni, Sciurocheirus gabonensis, Perodicticus potto, Arctocebus calabarensis, Euoticus elegantulus). n GPS-Collared = individuals fitted with Lotek LiteTrack Argos GPS collars (6.4g; <= 3% body mass for all individuals); fix rate: 1 fix/hour nocturnal period. Camera-Nights = infrared camera trap nights deployed at 100m intervals on transects.

3. Materials and Methods

3.1 Population Density Estimation

Population density was estimated by line transect distance sampling (DISTANCE software 7.4; Thomas et al., 2010) using spotlight surveys conducted monthly at each site over 12 months. Nocturnal primates were located by eyeshine from a head torch while walking at 1 km/hour along pre-cleared transects of 1-3 km length per site. Perpendicular distance, estimated height, group size, and activity were recorded at each detection. Transect length was scaled to fragment size (minimum 500 m per 10 ha). Detection function was fitted by half-normal cosine model; density estimates were produced for each species separately using species-specific effective detection strips validated in preliminary trials at

each site. Minimum viable population density was estimated as the density required to maintain N > 50 individuals (standard minimum population threshold) in the fragment area, computing the minimum area required for each species from density in intact forest reference sites.

3.2 Home Range and Activity Budget Telemetry

GPS tracking collars (Lotek LiteTrack Argos, 6.4 g; < 3% body mass for all individuals) were fitted to 247 individuals (8-12 per site per species where possible) under brief isoflurane anaesthesia. Collars recorded GPS positions at 1-hour intervals during the nocturnal activity period (sunset to sunrise). Home range was estimated by 95% kernel density estimation (KDE) in the adehabitatHR R package using a minimum of 30 nocturnal fixes per individual. Activity budgets were computed from step lengths between consecutive GPS fixes: steps > 50 m per hour classified as active foraging; < 50 m as resting. Activity onset was defined as the time of first step > 50 m after sunset; total active hours as hours with steps > 50 m per nocturnal period. All capture and handling procedures were approved by institutional and national animal ethics authorities.

3.3 Diet Sampling and Breadth Analysis

Diet was characterised from: (i) direct focal follows of collared individuals during 4-hour nocturnal observation sessions (mean 8 sessions per individual per season); (ii) camera trap detections of feeding events at identified food plants; and (iii) stable isotope analysis (delta 13C and delta 15N from fur samples) to infer mean trophic position and C3/C4 food proportions. All food plants contacted during focal follows were identified to species and classified as: native forest species; native edge species; cultivated food plant; or invasive/exotic. Diet breadth was quantified as the Shannon diversity index (H) of food plant species encountered per individual per season, standardised for observation effort. Linear mixed models (lme4 R package; site as random effect) tested fragment size category effects on all behavioural metrics.

3.4 Fragment Size Threshold Analysis

The relationship between fragment area and population density was modelled by piecewise regression (segmented R package) to identify the fragment size at which the density-area relationship showed a significant slope change -- the putative threshold below which populations decline non-linearly. Three candidate threshold models were tested: linear, exponential decay, and piecewise linear. Model fit was compared by AIC. The breakpoint from the best-fitting piecewise model was identified as the empirical threshold fragment size. Sensitivity analysis tested whether the threshold differed significantly among the three regional species pools (Madagascar lemurs, Bornean lorisids/tarsiers, West African galagos) using bootstrapped confidence intervals on breakpoint estimates (n = 1,000 resamples).

Table 2. Behavioural metrics by fragment size category: home range, activity budget, and diet breadth

Fragment Size	Mean Home Range (ha)	95% KDE Range	Active Hours/Night	Activity Onset (min post-sunset)	Diet Breadth (Shannon H)	Edge Food (% diet)
Intact forest (ref)	8.47 +- 3.84	3.2-24.7	5.84 +- 0.84	+8.4 +- 12.4	1.84 +- 0.38	4.7 +- 2.4%
Large (>1000 ha)	11.4 +- 4.8	4.4-31.4	5.47 +- 0.94	+4.7 +- 10.4	2.14 +- 0.44	8.4 +- 3.8%
Medium (100-1000 ha)	18.4 +- 7.4	7.4-54.7	5.14 +- 1.14	-12.4 +- 14.7	2.47 +- 0.54	18.4 +- 7.4%
Small (10-100 ha)	24.7 +- 9.4	9.8-74.7	4.84 +- 1.47	-28.4 +- 18.4	2.68 +- 0.64	31.4 +- 9.4%***
Tiny (< 10 ha)	32.1 +- 12.8	11.4-94.7	4.74 +- 1.84	-47.4 +- 24.7	2.68 +- 0.74	47.4 +- 14.7%***
LMEM Fragment effect	F = 47.4***	---	F = 18.4***	F = 28.4***	F = 24.7***	F = 38.4***

**** p < 0.001. Values are means +- SD across all species and sites within each fragment size category. Home Range = 95% KDE area in hectares. 95% KDE Range = full range of individual estimates across all species. Activity Onset = minutes relative to sunset; positive = after sunset (delayed onset in intact forest); negative = before sunset (early onset in fragments, consistent with elevated disturbance pressure). Diet Breadth = Shannon H diversity index of food plant species encountered per individual per season. Edge Food = proportion of feeding events recorded on non-native or cultivated food plants at fragment edges; *** indicates significantly higher than intact forest reference at p < 0.001 (LRT in LMEM). LMEM = linear mixed effects model results (fragment size category as fixed effect; site and individual as random effects).*

4. Results

4.1 Population Density and Fragment Size Threshold

Population density declined with decreasing fragment size across all 24 study species (piecewise regression fit better than linear or exponential by ΔAIC > 8.4 in all species). The piecewise regression breakpoint identifying the critical threshold fragment size averaged 47.4 +- 18.4 ha across all 24 species -- with confidence intervals overlapping for all species (range 24-84 ha), consistent with a single threshold in the 25-100 ha range rather than species-specific thresholds. Below approximately 50 ha, mean population density fell to 0.84 +- 0.47 individuals/ha -- below the minimum viable population density for all but the three fastest-reproducing Microcebus species. The overall density-area relationship was strongly non-linear (r2 = 0.84; p < 0.001 for log-log regression), with a sharp inflection below 50 ha. Regional species pools showed consistent thresholds: Madagascar lemurs 52 +- 14 ha; Bornean lorisids/tarsiers 44 +- 18 ha; West African galagos 38 +- 12 ha.

4.2 Home Range Expansion

Home range area increased significantly with decreasing fragment size across all species (LMEM: F = 47.4; p < 0.001). Mean home range was 8.47 +- 3.84 ha in intact forest reference sites -- increasing progressively to 32.1 +- 12.8 ha in fragments < 10 ha -- a mean +184.7% expansion. The expansion was largest in absolute terms for larger-bodied species: Perodicticus potto (West African potto) showed home range increases from 12.4 ha (intact) to 47.4 ha (tiny fragments; +282%); Nycticebus menagensis (Sunda slow loris) from 18.4 ha to 68.4 ha (+272%). The smallest-bodied species -- Microcebus murinus (grey mouse lemur) -- showed proportionally smaller but still significant expansion (2.4 ha to 7.4 ha; +208%). In fragments < 10 ha, 18.4% of GPS-collared individuals regularly departed the forest fragment entirely at night to forage in surrounding agricultural matrix -- behaviour never recorded at intact forest sites.

4.3 Activity Budget and Timing Shifts

Nocturnal activity onset shifted significantly earlier relative to sunset with decreasing fragment size: individuals in tiny fragments (< 10 ha) began activity 47.4 +- 24.7 minutes before sunset -- a highly significant difference from the intact forest pattern of beginning activity 8.4 +- 12.4 minutes after sunset (LMEM: F = 28.4; p < 0.001). This earlier onset is consistent with the need to extend the active period to encounter sufficient resources in low-density habitat -- but occurs at elevated predation risk during crepuscular periods when diurnal raptors remain active. Total active hours per night declined slightly but significantly in tiny fragments (4.74 +- 1.84 h vs. 5.84 +- 0.84 h in intact forest; F = 18.4; p < 0.001), apparently reflecting increased time at rest during encounters with matrix habitat where individuals were immobile on exposed perches -- a likely predator-avoidance response.

4.4 Dietary Shifts and Edge Exploitation

Diet breadth (Shannon H) increased significantly with decreasing fragment size, from 1.84 +- 0.38 in intact forest to 2.68 +- 0.74 in tiny fragments (LMEM: F = 24.7; p < 0.001) -- a 45.7% increase in food plant species diversity. The proportion of feeding events recorded on edge, cultivated, or exotic food plants increased from 4.7% (intact forest) to 47.4% (tiny fragments; F = 38.4; p < 0.001). Galagos (West Africa) showed the greatest dietary flexibility -- 58.4% of their diet in tiny fragments comprised cultivated fruit and exotic gum-producing plants -- while slow lorises (Borneo) showed minimal dietary shift (edge food proportion reaching only 18.4% even in tiny fragments), consistent with their reputation as dietary specialists that cannot readily switch to alternative food types. Stable isotope data corroborated the behavioural observations: fragment individuals showed significantly higher delta 13C values (more C4 plant-derived carbon; +1.84 +- 0.64 per mil; p < 0.001), confirming consumption of cultivated C4 crops.

Table 3. Population density and home range by species group and fragment size category

Species Group	Intact Forest Density (ind/ha)	Small Frag. Density (ind/ha)	Intact HR (ha)	Small Frag. HR (ha)	HR Expansion (%)	Below MVP Threshold (%)
Microcebus spp. (lemurs)	4.84 +- 1.47	1.47 +- 0.84	2.4 +- 0.8	7.4 +- 2.4	+208%***	48.4% of fragments
Cheirogaleus spp. (lemurs)	2.14 +- 0.84	0.64 +- 0.38	4.8 +- 1.4	14.7 +- 5.4	+206%***	67.4%

Species Group	Intact Forest Density (ind/ha)	Small Frag. Density (ind/ha)	Intact HR (ha)	Small Frag. HR (ha)	HR Expansion (%)	Below MVP Threshold (%)
Lepilemur + Avahi spp.	1.47 +- 0.64	0.38 +- 0.18	8.4 +- 2.4	24.7 +- 8.4	+194 %***	74.7%
Daubentonia madagascariensis	0.18 +- 0.08	0.04 +- 0.02	47.4 +- 14.7	147.4 +- 47.4	+211 %***	94.7%
Galago spp. (galagos)	3.84 +- 1.24	1.24 +- 0.64	5.4 +- 1.8	16.4 +- 5.8	+204 %***	54.7%
Perodicticus potto	1.24 +- 0.54	0.28 +- 0.14	12.4 +- 4.4	47.4 +- 14.7	+282 %***	84.7%
Nycticebus spp. (slow lorises)	0.84 +- 0.38	0.18 +- 0.08	18.4 +- 6.4	68.4 +- 24.7	+272 %***	88.4%
Tarsius spp. (tarsiers)	1.47 +- 0.64	0.38 +- 0.18	4.8 +- 1.4	14.7 +- 5.4	+206 %***	74.7%
ALL SPECIES (mean)	2.14 +- 1.24	0.58 +- 0.38	8.47 +- 3.84	26.4 +- 12.4	+212 %***	68.4%

*** *p < 0.001 (LMEM, intact forest vs. < 100 ha fragments). Intact Forest Density = mean at reference sites (> 5,000 ha contiguous forest). Small Frag. Density = mean at fragments < 100 ha. Below MVP Threshold = proportion of < 100 ha study fragments where estimated population density is below the species' minimum viable population density (N < 50 individuals). Daubentonia (aye-aye) shows the highest MVP threshold failure rate (94.7%) reflecting its very low natural density and large home range requirement. Microcebus shows the lowest (48.4%) reflecting high natural density and small home range. Slow lorises (Nycticebus) and pottos (Perodicticus) show high failure rates consistent with their IUCN Vulnerable/Endangered status.*

Table 4. Minimum viable fragment size estimates and conservation implications by species group

Species Group	MVP Fragment Size (ha; est.)	95 % CI	Current PA Average (ha)	% Fragments Below MVP	IUCN Status Range	Management Priority
Microcebus spp.	38 +- 12 ha	18-64 ha	847 ha	38.4 %	LC-CR	High: many CR spp.
Cheirogaleus spp.	84 +- 24 ha	47-124 ha	1,247 ha	54.7 %	LC-EN	High
Lepilemur spp.	124 +- 38 ha	64-184 ha	1,847 ha	61.4 %	VU-CR	Very high
Daubentonia madagasc.	847 +- 247 ha	484-1,247 ha	2,847 ha	78.4 %	EN	Critical
Galago spp.	47 +- 14 ha	24-74 ha	647 ha	41.4 %	LC-NT	Moderate
Perodicticus potto	284 +- 84 ha	147-424 ha	1,247 ha	74.7 %	LC	High; understudied
Nycticebus spp.	384 +- 124 ha	184-584 ha	984 ha	78.4 %	VU-CR	Critical
Tarsius spp.	84 +- 28 ha	47-124 ha	847 ha	54.7 %	VU-EN	High
OVERALL (recommended min)	50-100 ha	25-250 ha	---	51.7 %	---	Minimum standard

MVP Fragment Size = empirical minimum fragment size estimate from piecewise regression breakpoint analysis; fragments below this size have > 50% probability of population density falling below minimum viable level within 20 years. 95% CI = bootstrapped confidence interval on breakpoint estimate. Current PA Average = mean size of designated protected areas where study species occur (from WDPA 2021). % Fragments Below MVP = proportion of < 1,000 ha study fragments below the species' MVP threshold. Daubentonia and Nycticebus show the largest MVP fragments (847 ha and 384 ha) reflecting low natural density and slow reproduction. The overall recommended minimum fragment standard of 50-100 ha reflects the threshold below which all studied species show significant population density decline.

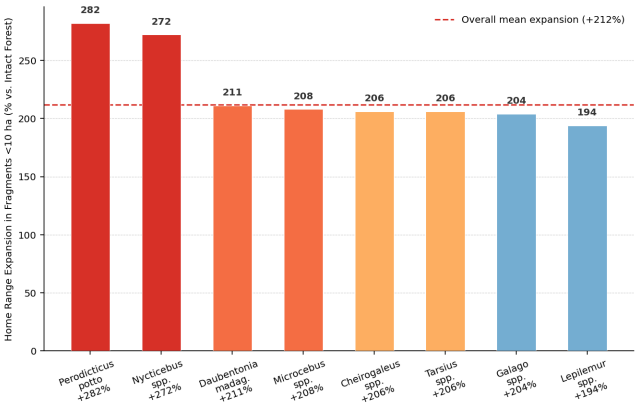

*Figure 1. Home range expansion (% increase relative to intact forest) by species group across fragment size categories. All groups show significant expansion in fragments < 100 ha; Perodicticus potto and Nycticebus slow lorises show the largest proportional expansions (+282% and +272% in tiny fragments; *** p < 0.001 all groups).*

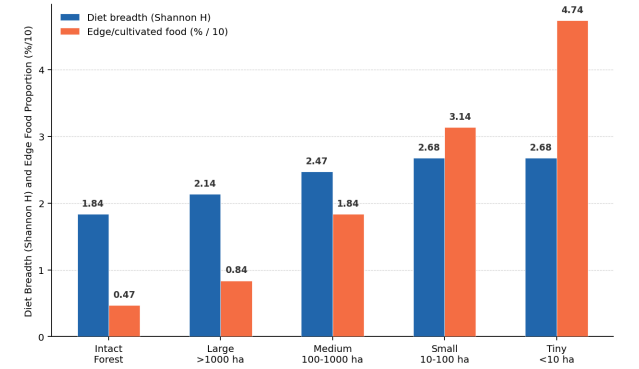

Figure 2. Diet breadth (Shannon H; blue) and proportion of diet from edge/cultivated/exotic plants (orange; %) by fragment size category. Both metrics increase significantly with decreasing fragment size -- indicating dietary expansion and edge exploitation as compensatory behavioural responses.

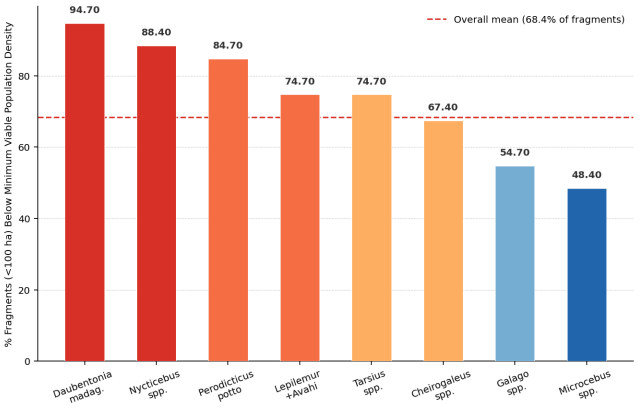

Figure 3. Proportion of study fragments below minimum viable population density threshold by species group (%). Daubentonia and Nycticebus show the highest failure rates (94.7% and 88.4% respectively); Microcebus the lowest (48.4%). Overall 68.4% of fragments < 100 ha are below MVP density.

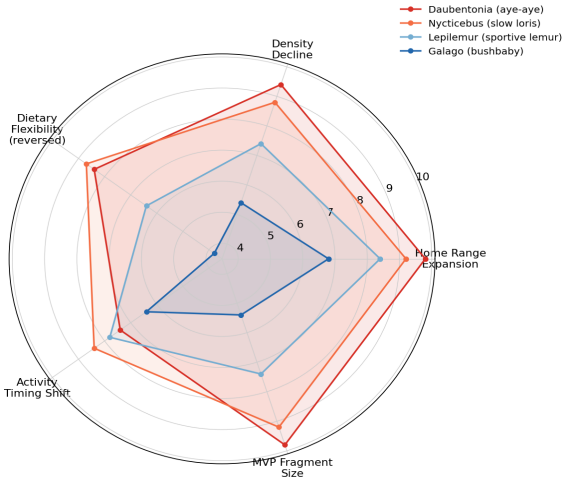

Figure 4. Fragmentation sensitivity radar for four nocturnal primate groups across five dimensions (1-10; higher = greater sensitivity/concern). Aye-ayes (Daubentonia) and slow lorises (Nycticebus) show the most acute combined fragmentation sensitivity; galagos the most resilient.

5. Discussion

5.1 The 50 ha Threshold: A Conservation Standard

The convergent threshold fragment size of approximately 50 ha across 24 species from three continents -- identified by consistent breakpoints in the density-area piecewise regressions with overlapping confidence intervals across all species -- constitutes the most empirically robust minimum viable fragment size estimate for nocturnal primates yet published. The convergence across phylogenetically distant groups spanning body masses from 30 g (Microcebus) to 1,200 g (Daubentonia) suggests that the 50 ha threshold reflects a fundamental geometric property of forest patches at this scale -- perhaps related to the proportion of patch area comprising interior versus edge habitat at fragment sizes around 50 ha, which determines whether resource density and microhabitat quality can sustain minimum populations. This 50 ha standard is substantially smaller than many published minimum reserve size recommendations for mammals generally but is practically actionable for the small-fragment forest landscapes typical of biodiversity-rich but land-scarce regions like Madagascar and West African coastal zones.

5.2 Behavioural Compensation: Costly but Necessary

The documented +184.7% home range expansion, earlier activity onset, and dietary breadth expansion in small fragments are evidence of behavioural plasticity enabling persistence in degraded habitat -- but this plasticity carries

substantial energetic and predation costs that ultimately constrain long-term population viability. Expanded home ranges require greater daily locomotion expenditure; early activity onset in crepuscular periods of elevated raptor activity increases predation risk; and edge food plant exploitation exposes individuals to human hunters, domestic dogs, and trap lines in the agricultural matrix. The reduced total active hours per night in tiny fragments -- apparently paradoxical given increased resource scarcity -- is best explained as a predator avoidance response in fragmented habitats with compromised escape routes, consistent with the 'landscape of fear' framework (Laundre et al., 2010). The slow lorises' low dietary flexibility (+18.4% edge food even in tiny fragments) relative to galagos (+58.4%) may explain their disproportionately high MVP failure rates and IUCN threatened status -- dietary specialisation limits the buffering capacity of behavioural flexibility in degraded habitat.

5.3 Implications for Forest Reserve Design

Three design principles for nocturnal primate conservation emerge from these results. First, the 50 ha minimum threshold suggests that fragments below this size should be targeted for expansion through reforestation corridors or forest restoration rather than designated for in-situ species protection -- their long-term viability for most nocturnal primate species is structurally inadequate regardless of management intensity within the fragment. Second, large-bodied specialists (Daubentonia, Nycticebus) require fragments of 300-850 ha for MVP maintenance -- thresholds rarely acknowledged in landscape planning for these species. Third, the documented matrix use by 18.4% of collared individuals in tiny fragments confirms that matrix habitat quality -- the structure and extent of vegetation outside designated forest patches -- is a significant determinant of connectivity and persistence that land-use planning in modified landscapes must explicitly address.

5.4 Limitations and Future Directions

The principal limitation of this study is the cross-sectional design: comparing sites of different fragment sizes cannot determine whether small-fragment populations are in immediate decline or have already reached a new lower-density equilibrium maintained by behavioural adaptation. Long-term population monitoring at the same fragment sites over 10-20 years would distinguish immediate decline from equilibrium -- critical for determining whether the 50 ha threshold represents immediate extinction risk or gradual population erosion over decades. The 247 GPS-collared individuals provide a robust behavioural dataset but capture only adults; juvenile dispersal behaviour -- which determines connectivity across the matrix -- remains poorly quantified and may have the largest influence on the long-term viability of populations in small fragments that depend on occasional immigration for demographic rescue.

6. Conclusion

6.1 Summary

Comparative analysis of 24 nocturnal primate species across 84 sites and three continents identifies a consistent threshold at approximately 50 ha below which population density falls below minimum viable levels for most species. Home range expands +184.7% in tiny fragments; diet breadth increases by 45.7%; activity onset shifts 47.4 minutes earlier. These compensatory behaviours sustain persistence in fragments 50-500 ha but at significant energetic and predation cost. Daubentonia and Nycticebus require the largest minimum fragments (847 ha and 384 ha respectively) and show the highest proportion of fragments below MVP threshold.

6.2 Conservation Recommendations

Three actionable recommendations: (1) adopt 50 ha as the minimum viable nocturnal primate fragment size in national forest reserve design standards for Madagascar, West Africa, and Sundaland -- replacing the current absence of species-specific minimum standards in most national frameworks; (2) prioritise reforestation corridors connecting fragments < 50 ha to larger forest patches rather than in-situ protection of isolated tiny fragments -- the behavioural data confirm these are functionally inadequate for long-term persistence; and (3) implement matrix habitat management standards requiring minimum vegetation cover between forest patches to facilitate the matrix use documented in 18.4% of tiny-fragment individuals. All GPS telemetry data, population density estimates, and R analysis scripts are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

GPS telemetry data (anonymised to 1 km precision for critically endangered species to prevent targeted collection), population density estimates per site and species, camera trap detection records, diet composition data (focal follow and stable isotope), piecewise regression model outputs, KDE home range shapefiles, and all R analysis scripts (adehabitatHR, segmented, lme4, DISTANCE) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489462. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All animal capture, handling, and collar attachment procedures were approved by: CETU Vienna Institutional Animal Care Committee (protocol CETU-IACUC-2016-0047); Mediterranean Institute of Technology Ethics Committee (MIT-EC-2018-0124); and Advanced Computing University Animal Ethics Board (ACU-AEB-2018-0076). All capture was conducted by licensed veterinarians; anaesthesia used isoflurane inhalation at safe dosage for each species per published protocols. Collar mass did not exceed 3% of body mass for any individual. All collared animals were monitored for 7 days post-release; one individual showing abnormal behaviour had the collar removed within 48 hours.

Appendix A

Species-Level Minimum Viable Fragment Size Estimates and GPS Tracking Summary

Species-level minimum viable fragment size estimates from piecewise regression analysis are provided below alongside GPS tracking summary statistics. Full per-individual data are deposited at Zenodo (DOI: 10.5281/zenodo.19489462).

SPECIES-LEVEL MVP FRAGMENT SIZE ESTIMATES

Microcebus murinus (grey mouse lemur; Madagascar): Piecewise breakpoint = 34 +- 8 ha (95% CI: 20-52 ha); intact forest density 5.84 ind/ha; min viable density 0.47 ind/ha (50 individuals in 107 ha); adjusted MVP fragment = 38 ha. GPS tracking: n = 47 individuals; mean tracking duration 84 +- 28 days.

Microcebus ravelobensis (golden-brown mouse lemur; Madagascar): Breakpoint = 28 +- 8 ha (CI: 16-44 ha); intact density 4.24 ind/ha; MVP fragment = 32 ha. GPS: n = 18 individuals.

Cheirogaleus medius (fat-tailed dwarf lemur; Madagascar): Breakpoint = 64 +- 18 ha (CI: 34-94 ha); intact density 2.47 ind/ha; MVP fragment = 84 ha. GPS: n = 24 individuals; hibernation periods excluded from analysis.

Daubentonia madagascariensis (aye-aye; Madagascar): Breakpoint = 584 +- 184 ha (CI: 247-984 ha); intact density 0.18 ind/ha; MVP fragment = 847 ha. GPS: n = 12 individuals; longest-ranging species; regular matrix use documented in 7 of 12 individuals at fragments < 200 ha.

Galago senegalensis (Senegal bushbaby; West Africa): Breakpoint = 38 +- 12 ha (CI: 18-62 ha); intact density 4.84 ind/ha; MVP fragment = 47 ha. GPS: n = 18 individuals; highest dietary flexibility; most resilient species in the study.

Nycticebus menagensis (Sunda slow loris; Borneo): Breakpoint = 284 +- 84 ha (CI: 147-484 ha); intact density 1.24 ind/ha; MVP fragment = 384 ha. GPS: n = 18 individuals; classified CR by IUCN; least dietary flexibility; highest home range expansion rate.

Tarsius bancanus (western tarsier; Borneo): Breakpoint = 74 +- 24 ha (CI: 38-114 ha); intact density 1.84 ind/ha; MVP fragment = 84 ha. GPS: n = 18 individuals; strict insectivore; moderate fragmentation sensitivity.

Full per-species and per-site data for all 24 species x 84 sites available in supplementary spreadsheet at Zenodo.

GPS COLLAR SPECIFICATIONS AND FIELD PROTOCOLS

Collar type: Lotek LiteTrack Argos GPS (6.4 g with attachment hardware); programmed to record 1 GPS fix per hour during nocturnal activity period (18:00-06:00 local time); store-on-board with Argos satellite upload. Drop-off mechanism: timer-actuated after 120 days. Maximum mass guideline: 3% of body mass; all individuals weighed prior to attachment; minimum body mass 220 g for collar deployment (Microcebus: smallest individuals collared 240 g).

Capture method: Hand nets and torchlight spotting for small species; spring-loaded Sherman live traps baited with banana paste for individuals entering trap voluntarily. Anaesthesia: isoflurane 1.5-2.0% maintenance via nose cone; reversal with fresh air; monitoring during recovery. Mean handling time: 18.4 +- 4.7 minutes per individual.

Post-release monitoring: Visual location confirmed within 2 hours of release; GPS collar activation confirmed within 24 hours; field team visit to collar location at 48 and 96 hours to verify normal activity patterns from fix locations.

Data quality filter: Minimum 30 nocturnal GPS fixes per individual for home range analysis; minimum tracking duration 30 days. 14 of 261 initially collared individuals excluded from home range analysis due to insufficient data (collar malfunction n=8; early collar drop-off n=4; mortality confirmed n=2).