




Arboreal Lemur Terrestriality is Influenced by When and Where Predators are Present

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Abstract

It is thought arboreal species avoid foraging on the ground due to perceived predation risk, making the study of when and where arboreal species use the ground key in understanding foraging versus safety tradeoffs. We used publicly available, opportunistic, camera-trap observations from surveys across Madagascar to examine whether arboreal lemur ground use was spatially and temporally related to fosa (*Cryptoprocta ferox*), a native predator, and human presence. We observed 14 species of diurnal lemur ($n=287$ individual observations) and six species of nocturnal lemur ($n=105$ individual observations). With static two-species occupancy models and kernel density estimation, we found diurnal and nocturnal lemur ground use was spatially and temporally related to fosa presence. Diurnal lemurs used the ground less at camera locations where fosa were present compared to camera locations where they were absent, particularly if those camera locations lacked other native carnivores. Nocturnal lemurs used the ground more at camera locations fosa were observed at within the past 5 days compared with camera locations where fosa were not observed at within the past 5 days. Despite humans and diurnal lemurs being active at the same time 80% of the diel cycle (temporal overlap $\Delta=0.80$; 95% confidence interval [CI]: 0.75–0.85), diurnal lemur spatial or temporal use of the ground and human presence were unrelated. Diurnal lemur temporal overlap with humans at camera locations where fosa were uncommon was higher ($\Delta=0.79$; 95% CI: 0.71–0.86) compared with where fosa were common ($\Delta=0.57$; 95% CI: 0.46–0.66). Future research on how arboreal lemurs navigate ground use in a multipredator landscape should include behavioral observations to better understand animal decision-making.

Keywords Terrestriality · Arboreality · Predation risk · Co-occurrence · Madagascar · Camera trapping

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Introduction

Primate researchers have long noted terrestriality in arboreal primates, but primatologists are just recently beginning to study this in earnest (Barnett *et al.*, 2012b; Eppley *et al.*, 2022). Arboreal primates are thought to avoid the ground out of fear of predation, with perceived predation risk influencing the nature and duration of ground use (Barnett *et al.*, 2012b). For example, golden-backed uakari (*Cacajao melanocephalus ouakary*) only foraged on the ground at patches closer to arboreal refuges and further from dense ground-based vegetation, presumably to avoid ambush (Barnett *et al.*, 2012a). Despite the danger of terrestrial predators, arboreal primates use the ground to avoid predation by flying/arboreal predators (Barnett *et al.*, 2012b), to forage (Souza-Alves *et al.*, 2019, 2021), to reduce energy expenditure when sleeping (Samson & Hunt, 2012) or foraging (Eppley *et al.*, 2016a), and to avoid intraspecific competition and hostility (Campbell *et al.*, 2005; Williamson *et al.*, 2021). As habitat degradation and climate change continues, arboreal primates might increase using the ground for resource acquisition and thermoregulation needs (Eppley *et al.*, 2022; Souza-Alves *et al.*, 2019), increasing their likelihood that terrestrial predators kill them at higher rates and add pressure to already threatened populations. Understanding how arboreal primate ground use is influenced by their perception of predation risk is therefore important in this changing world.

Lemurs, endemic to the island nation of Madagascar, are in decline, with extinction threatening 87% of species (Estrada *et al.*, 2017). Arboreal lemur species occasionally come to the ground for foraging (Eppley *et al.*, 2016a), sleeping (Eppley *et al.*, 2016b; Ramananjato *et al.*, 2022), and hibernation (Blanco *et al.*, 2013). While a few studies suggested that predation risk influences lemur terrestriality (LaFleur *et al.*, 2014), none to our knowledge have investigated how direct predator presence influences their ground use. Fosa (*Cryptoprocta ferox*) are the largest native carnivore in Madagascar and prey on a variety of lemur species (Goodman *et al.*, 1997; Hawkins, 1998; Karpanty & Wright, 2007; Lührs & Dammhahn, 2009; Schnoell & Fichtel, 2011); thus, their presence should influence lemur terrestriality. Hunting also threatens lemurs (Borgerson, 2015; Borgerson *et al.*, 2016; Brook *et al.*, 2019), making it likely that lemurs would see humans as a predator to be avoided, as many species across the world do (Gaynor *et al.*, 2018; Suraci *et al.*, 2019; Tucker *et al.*, 2018). Prey often perceive humans as more dangerous than their natural predators (McComb *et al.*, 2011, 2014; Smith *et al.*, 2017; Widén *et al.*, 2022; Zanette & Clinchy, 2020), making it possible that human presence has a larger effect on lemur terrestriality compared with fosa presence.

To that end, we used opportunistic observation data collected via camera trap surveys to investigate how humans and fosa affect arboreal lemur ground use. We attempted to answer three questions:

1. Do fosa influence lemur spatial or temporal ground use?
2. Do humans influence lemur spatial or temporal ground use?
3. Does the level of human use (high vs. low) at a location influence the effect of fosa presence on lemur terrestrial spatiotemporal use and vice versa?

Although fosa do hunt arboreally—and humans are able to shoot lemurs in trees—we assume that arboreal lemurs would feel safer in the trees in areas that humans and fosa use, reducing their terrestriality. We hypothesized that lemurs would see humans as predators and predicted that diurnal lemurs would avoid using the ground at camera locations where humans were present, because human use of forests tends to be diurnal (Farris *et al.*, 2015a), causing their activity to temporally overlap with diurnal lemurs. Meanwhile, we predicted that nocturnal lemurs would not avoid using the ground due to human presence, because their time of activity naturally occurs when humans are not active. We hypothesized that lemurs would see fosa as predators but predicted that diurnal lemur ground use would not be influenced by fosa presence, because fosa tend to be cathemeral with crepuscular peaks of activity (Amoroso *et al.*, 2020; Farris *et al.*, 2015a; Merson *et al.*, 2018), making it less likely diurnal lemurs and fosa would overlap in time. Because the time of nocturnal lemur activity overlaps with fosa activity, we predicted that nocturnal lemur ground use would be spatially and temporally affected by fosa. Finally, we hypothesized that lemurs would fear humans as predators more than fosa and predicted that they would avoid using the ground more often at camera locations of high human use compared with areas of high fosa use. We also hypothesized that fosa would avoid camera locations where humans are present and so predicted that the influence of fosa presence on lemur terrestriality would be lower at camera locations with high human use (Farris *et al.*, 2016).

Methods

We used publicly available camera trap data from opportunistic surveys conducted in nine distinct protected areas across Madagascar (Wampole *et al.*, 2022 Metadata Fig. 1) between 2007 and 2021. Researchers placed camera traps at 1,156 locations comprising 38 independent surveys for terrestrial wildlife in eastern, humid rainforest and western, dry, deciduous forests. Overall, surveys ran for more than 60,000 trap nights and collected more than 100,000 observations of 103 species. For more information on camera setup, survey-specific length and sampling scheme, and other details, see Wampole *et al.* (2022). We compiled 392 observations of 20 lemur species across 21 surveys (2007 to 2021) in seven protected areas (Table I).

Our normalized, uncorrelated ($R^2 < 0.7$) covariates included distance to the nearest human structure or road, taken from Wampole *et al.* (2022), and the relative abundances of non-fosa native carnivores (bokiboky *Mungotictis decemlineata*, spotted fanaloka *Fossa fossana*, ring-tailed vontsira *Galidia elegans*, broad-striped vontsira *Galidictis fasciata*, brown-tailed vontsira *Salanoia concolor*, and falanouc *Eupleres goudotii*), nonnative carnivores (dogs *Canis familiaris*, cats *Felis silvestris*, and small Indian civets *Viverricula indica*), humans, and nonnative ungulates (zebu *Bos indicus*, goat *Capra hircus*, bushpig *Potamochoerus larvatus*, and horse *Equus caballus*). We estimated relative abundances—a rate of “use” of a location by a species—by dividing the total number of independent observations for that species/species category at that camera location by how long the camera location was active (trap-nights). We Researchers assumed observations were independent if two

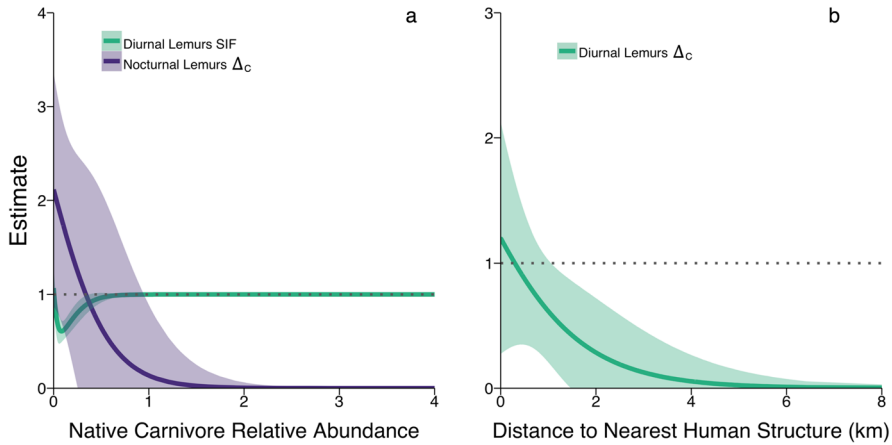


Fig. 1 Lemur spatiotemporal associations with fosa at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021. Diurnal lemur terrestrial co-occurrence (SIF) and nocturnal lemur terrestrial co-detection (Δ_c) with fosa (a) and how it varies over native carnivore relative abundance. Diurnal lemur terrestrial co-detection with fosa (b) and how it varies with distance from the nearest human structure (e.g., village or road). The dotted line indicates where co-occurrence or co-detection goes from avoidance (< 1) to attraction (> 1). Shaded areas are 85% confidence intervals.

observations of the same species/species category did not occur within the same 30-min period (Wampole *et al.*, 2022).

Because we were not looking for species-specific patterns in antipredator behavior, we grouped all species into a “diurnal” or “nocturnal” category. We determined whether lemurs were diurnal or nocturnal by looking at the literature (Mittermeier *et al.*, 2010) and conducting kernel density estimations by using package activity (Rowcliffe, 2021) in R (v 4.1.2; R Core Team, 2021) to characterize observed activity pattern for each identified species. We characterized lemur observations that were not identified to species with 1.57–4.71 rad values as “diurnal” and the rest as “nocturnal.” We limited our analyses to “diurnal” and “nocturnal” and did not include other potential categories (e.g., crepuscular) in the interest of having enough data to make our spatial models certain of converging.

Statistical Analyses

We ran two-species occupancy models using RPresence (v 2.13.41; MacKenzie & Hines, 2022) to characterize spatial co-occurrence patterns between lemurs and humans and fosa across 791 camera locations. We originally ran the multi-season parameterization but settled on the single-season parameterization due to data sparseness. Occupancy models estimate multiple parameters, including occupancy and detection probability (MacKenzie *et al.*, 2002). Occupancy probability is the probability a species of interest is present at/occupies the survey location; in our case, the probability a lemur uses the ground. Detection probability is the probability of detecting the species of interest, given it occupies the survey location; in our

Table 1 Summary of fosa, human, and diurnal and nocturnal lemur observations at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021

Activity category	Species	No. observations
Diurnal lemurs (n = 287)	<i>Cryptoprocta ferox</i>	1,276
	<i>Homo sapiens</i>	14,504
	<i>Eulemur albifrons</i>	29
	<i>E. collaris</i>	17
	<i>E. fulvus</i>	53
	<i>E. rubriventer</i>	5
	<i>E. rufifrons</i>	16
	<i>E. sanfordi</i>	1
	<i>Hapalemur griseus</i>	21
	<i>H. occidentalis</i>	6
	<i>Hapalemur spp.</i>	21
	<i>Propithecus candidus</i>	4
	<i>P. diadema</i>	5
	<i>P. edwardsi</i>	2
<i>Varecia rubra</i>	2	
Nocturnal lemurs (n = 105)	Unidentified species	105
	<i>Cheirogaleus major</i>	1
	<i>Daubentonia madagascarensis</i>	10
	<i>Lepilemur fleuretae</i>	16
	<i>L. microdon</i>	1
	<i>Lepilemur spp.</i>	19
	<i>Microcebus spp.</i>	8
	Unidentified species	50

case, the probability we detect a lemur, given it is using the ground. The two-species model assumes one species (species A) can influence the occupancy and detection probabilities of another (species B) and estimates two co-occurrence parameters: the species interaction factor (SIF), a measure of co-occurrence that considers spatial patterns of detection, and delta (Δ_C), a measure of co-detection that considers spatial and temporal patterns of detection simultaneously (Richmond *et al.*, 2010). In our models, lemurs were always species B.

SIF is estimated by

$$\frac{\psi^A \psi^{BA}}{\psi^A (\psi^A \psi^{BA} + (1 - \psi^A) \psi^{Ba})}$$

where ψ^A is the occupancy probability of species A, ψ^{BA} is the occupancy probability of species B given species A is present, and ψ^{Ba} is the occupancy probability of species B given species A is absent. The co-detection factor (Δ_C) is estimated by

$$\frac{r^{BA}}{r^A r^B}$$

where r^{BA} is the probability of detecting species A and B at the same location in the same survey occasion (i.e., five trap nights), r^A is the probability of detecting species A given species B is present at the same location, and r^B is the probability of detecting species B given species A is present at the same location (Table II). Co-occurrence (SIF) and co-detection (Δ_C) estimates > 1 indicate spatial or spatiotemporal co-occurrence more than would be expected at random, or a spatial or spatiotemporal “attraction,” respectively. Estimates < 1 indicate spatial or spatiotemporal co-occurrence less than would be expected at random (i.e., “avoidance”) and estimates equal to 1 indicate spatial or spatiotemporal “independence.” Despite using terms, such as “avoidance” and “attraction,” these models only analyze spatiotemporal patterns in species observations, which may or may not be influenced by behavior.

As many surveys ran for more than 3 months, we only included the first 64 trap nights of each survey to meet the demographic closure assumption. Although much spatiotemporal behavior occurs at finer temporal scales, we collapsed five trap nights into one survey occasion and estimated co-detection at a 5-day scale to improve model convergence. We used a stepwise approach when running our single-season, two-species, occupancy models. We first determined what covariates most strongly influenced detection of lemurs on the ground by ranking them using AIC (Akaike, 1973; Burnham & Anderson, 2002) to make sure we were not confusing a relationship with habitat to a relationship with human or fosa presence. Next, we included interactions (i.e., human presence influencing lemur detection on the ground). Once we had determined the detection model that most strongly explained our data using AIC, we used the top detection model as a base to determine what covariates influenced lemur occupancy (i.e., ground use). Finally, we investigated whether human/fosa presence was related to lemur ground use and estimated SIF and Δ_C . We show all “competing” models—models with Δ AIC values ≤ 2.0 (Table III)—and detail

Table II Parameters estimated by static (single-season) two-species occupancy models

Type	Parameter	Definition
Occupancy	ψ_A	Occupancy probability of species A
	ψ_{BA}	Occupancy probability of species B at locations where species A is present
	ψ_{Ba}	Occupancy probability of species B at locations where species A is absent
	SIF	Species Interaction Factor, a measure of spatial co-occurrence
Detection	p_A	Detection probability of species A at locations where species B is absent
	r_A	Detection probability of species A at locations where species B is present
	p_B	Detection probability of species B at locations where species A is absent
	r_{BA}	Detection probability of species B at locations where species A is present and detected
	r_{Ba}	Detection probability of species B at locations where species A is present and not detected
	Δ_C	Co-Detection Factor, a measure of spatiotemporal co-occurrence

Table III Competing models ($\Delta AIC \leq 2.0$) from two-species occupancy analyses investigating terrestrial spatial interactions between lemurs and fosa and lemurs and humans at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021. ψ is occupancy; p is detection of either species when the other species is absent; r is detection of either species when the other species is present

Dominant species (A)	Subordinate species (B)	Model ^a	$\Delta AICc$	w	k	LogLike
Fosa	Diurnal Lemurs	$\psi_A(\text{ncarn}), \psi_{BA \neq \psi_{Ba}}(\text{ncarn}), P_{A \neq r_A}(\text{disthumhab}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{disthumhab})$	0.00	0.91	16	4410.66
		$\psi_A(\text{eung}), \psi_B(\text{eung}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	0.00	0.32	14	3994.57
	Nocturnal Lemurs	$\psi_A(\text{ncarn}), \psi_B(\text{ncarn}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	0.17	0.29	14	3994.74
		$\psi_A(\text{disthumhab}), \psi_B(\text{disthumhab}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	0.39	0.26	14	3994.96
Human	Diurnal Lemurs	$\psi_A(\text{human}), \psi_B(\text{human}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	1.99	0.12	14	3996.56
		$\psi_A(\text{ecarn}), \psi_{BA \neq \psi_{Ba}}(\text{ecarn}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	0.00	0.64	16	7648.21
	Nocturnal Lemurs	$\psi_A(\text{ecarn}), \psi_B(\text{ecarn}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	1.18	0.56	14	7653.54
		$\psi_A(\text{ecarn}), \psi_B(\text{ecarn}), P_{A \neq r_A}(\text{ncarn}), P_{B \neq r_{BA \neq r_{Ba}}}(\text{ncarn})$	0.00	1.00	14	7135.38

^a disthumhab—distance (km) to nearest human structure or road; ecarn—exotic carnivore relative abundance; human—human relative abundance; ncarn—native carnivore, excluding fosa, relative abundance

the results from the top model. We present 85% confidence intervals (Burnham & Anderson, 2002).

We investigated temporal interactions by converting clock times as recorded by camera traps to average-anchored radian values (Vazquez *et al.*, 2019) and quantifying diel activity patterns—or timing of ground use—of humans, fosa, diurnal, and nocturnal lemurs by using kernel-density estimation in package activity. We compared timing of ground use between species using bootstrapping (compareCkern) in package activity and bootstrapped temporal overlap (Δ)—the measure of the overlap between two species' diel activity patterns—estimates and 95% confidence intervals using package overlap (Ridout & Linkie, 2009). We used Δ_4 if the sample size for the species with the fewest detections was ≥ 75 ; otherwise, we used Δ_1 (Ridout & Linkie, 2009).

To examine the influence of habitat and other species' relative abundances on the timing of lemur ground use, we attempted to run linear-circular regression models in package activity using function “fitlincirc” on lemur activity data, but our models did not converge. Instead, we investigated differences in temporal overlap of ground use between humans and lemurs, and fosa and lemurs, at camera locations that were “high” and “low” in the use (relative abundance) of the opposite predator (e.g., human-lemur overlap at camera locations high and low in fosa relative abundance). For fosa, we classified camera locations as low if fosa non-zero relative abundance estimates were ≤ 0.03 ; otherwise, we classified them as high. For humans, we classified camera locations as low if nonzero human relative abundance were ≤ 0.21 ; otherwise, we classified them as high. We Bonferroni-corrected significance values to $p=0.0017$.

Ethical Note

This study used purely observational data from Wampole *et al.* (2022), and thus is in line with the Principles for the Ethical Treatment of Nonhuman Primates by the American Society of Primatologists (2001).

Data Availability The data analyzed in this study are published in Wampole *et al.* (2022) and publically available.

Results

We compiled 287 observations of 14 species of diurnal lemurs and 105 observations of six species of nocturnal lemurs for a total of 392 lemur observations (Table I). Fosa presence affected diurnal and nocturnal lemur ground use in ways contrary to our original predictions (Table IV). Fosa-diurnal lemur SIF estimates only dipped into avoidance from 0.025 to 0.37 observations of native carnivores a day (Fig. 1a). Fosa presence and detection did affect diurnal lemur detection on the ground, with fosa-diurnal lemur co-detection decreasing with increasing distance to the nearest

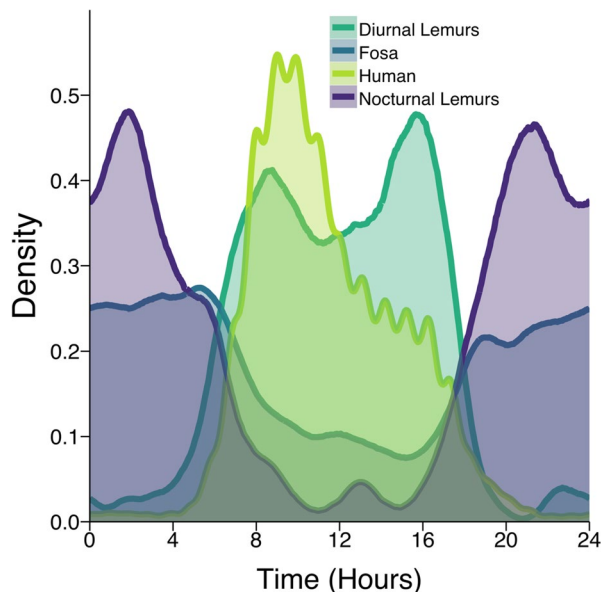
Table IV Summary of terrestrial spatiotemporal results between humans and lemurs and fosa and lemurs at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021. Spatial and spatiotemporal results come from two-species occupancy models. 0 indicates no effect, – indicates a negative effect, and + indicates a positive effect. Temporal overlap includes estimate and 95% confidence interval

Predator	Human		Fosa	
	Diurnal	Nocturnal	Diurnal	Nocturnal
Lemur				
Spatial ($\psi_{BA} \neq \psi_{Ba}$)	0/–		0/–	
Spatiotemporal ($r_{BA} \neq r_{Ba}$)			0/–	0/–
Temporal overlap	0.80 (0.75–0.85)	0.18 (0.10–0.20)	0.41 (0.34–0.42)	0.77 (0.69–0.83)

town/village/road (Fig. 1b). Meanwhile, fosa presence only affected nocturnal lemur detection on the ground. Fosa-nocturnal lemur co-detection was independent until native carnivore relative abundance reached 0.95 observations/day; then, it dipped into avoidance (Fig. 1a). Human relative abundance did not influence any fosa-lemur spatial co-occurrence and co-detection patterns (Table III).

Fosa and lemur activity patterns differed significantly (Fig. 2); as expected, fosa diel activity overlapped more with the timing of nocturnal lemur ground use ($\Delta=0.77$; 95% CI: 0.69–0.83) than the timing of diurnal lemur ground use ($\Delta=0.41$; 0.34–0.42), although fosa had a different center of activity (5:18 in the morning) compared with nocturnal lemurs (1:52 in the morning). The temporal overlaps between diurnal lemurs and fosa did not differ based on human relative abundance classes (Fig. 3d), nor did the temporal overlaps between nocturnal lemurs and fosa.

Fig. 2 Activity patterns of diurnal lemurs, fosa, humans, and nocturnal lemurs at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021.



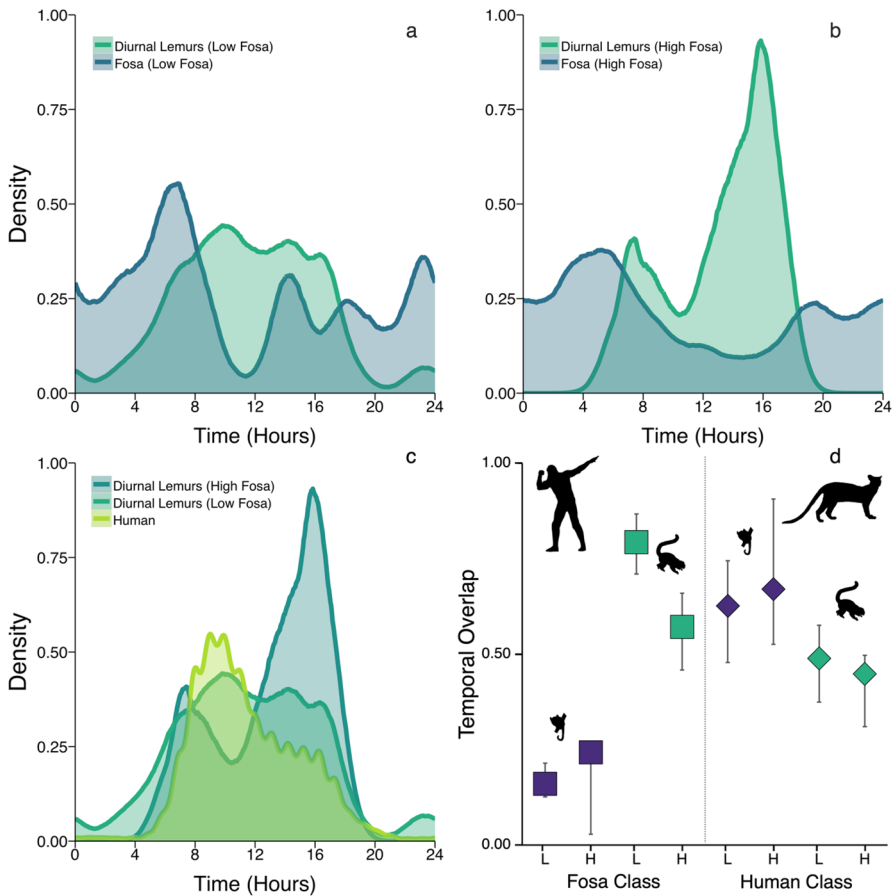


Fig. 3 Activity patterns and temporal overlap between diurnal lemurs, fosa, humans, and nocturnal lemurs at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021. Diurnal lemur and fosa activity patterns at locations where fosa relative abundance is low (≤ 0.03 ; **a**) or high (> 0.03 ; **b**) and human and diurnal lemur activity patterns at locations with low and high fosa relative abundance (**c**). Diurnal and nocturnal lemur temporal overlap with fosa (right side of **d**) at locations where human relative abundance was low (≤ 0.21) or high (> 0.21) and diurnal and nocturnal lemur temporal overlap with humans (left side of **d**) at locations where fosa relative abundance was low or high. Gray lines are 95% confidence intervals. Icons from phylopic.org.

As we predicted, diurnal lemurs and humans had an estimated $SIF < 1$ (i.e., “avoidance”) up until a value of 0.17 exotic carnivore relative abundance; for higher values, human-diurnal lemur spatial co-occurrence became independent (Fig. 4a). While diurnal lemur detection on the ground was lower at camera locations where humans were present compared with where humans were absent, human-diurnal lemur co-detection 85% confidence intervals overlapped 1 (Fig. 4b). Human presence did not influence nocturnal lemur ground use, but human-nocturnal lemur co-detection was positive below 0.16 native carnivore observations/day (Fig. 4b). Fosa relative abundance did not influence human-lemur spatial co-occurrence patterns (Table III).

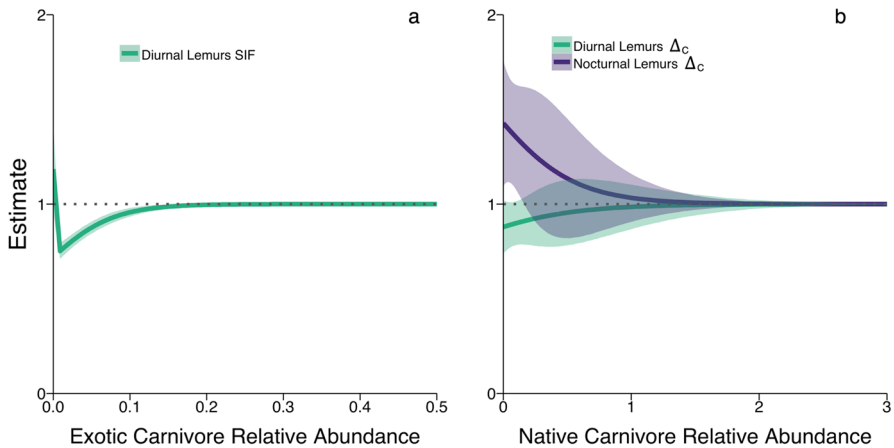


Fig. 4 Lemur spatiotemporal associations with humans at seven protected areas across Madagascar surveyed by Wampole *et al.* (2022) between 2007 and 2021. Diurnal lemur terrestrial co-occurrence (SIF; **a**) and co-detection (**b**) with humans as it varies across exotic (**a**) and native carnivore (**b**) relative abundance. Nocturnal lemur terrestrial co-detection with humans (**b**) as it varies across native carnivore relative abundance. Shaded regions are 85% confidence intervals and the gray dotted line at 1 indicates where co-occurrence/co-detection estimates go from attraction (> 1) to avoidance (< 1).

Human and lemur activity patterns also differed significantly (Fig. 2); as expected, human diel activity overlapped more with the timing of diurnal lemur ground use ($\Delta=0.80$; 95% CI: 0.75–0.85) than with the timing of nocturnal lemur ground use ($\Delta=0.18$; 95% CI: 0.10–0.20), although humans had a different peak in activity centered around 9:00 in the morning compared with diurnal lemurs (centered around 15:40 in the afternoon). Only human–diurnal lemur temporal overlap differed between fosa relative abundance classes, with human–diurnal lemur temporal overlap at camera locations with low fosa relative abundance ($\Delta=0.79$; 95% CI: 0.71–0.87) higher than at camera locations with high fosa relative abundance ($\Delta=0.57$; 95% CI: 0.46–0.66; Fig. 3d). At camera locations where fosa relative abundance was low, diurnal lemurs used the ground roughly the same amount between 6:00 am and 18:00 pm, whereas at camera locations where fosa relative abundance was high, diurnal lemurs had an activity peak at 15:50 in the afternoon (Fig. 3a–c).

Discussion

Fosa presence spatiotemporally influenced lemur ground use. Diurnal lemurs, which temporally overlapped with fosa to a moderate extent, were less likely to use the ground at camera locations where fosa were present, but only below a certain threshold of native carnivore relative abundance (aka, site use rate). We suggest that diurnal lemur ground use decreasing where fosa are present and where other native carnivores are rare might be connected to an unmeasured positive relationship between native carnivore relative abundance and the relative abundance of alternative prey (i.e., small mammals and birds). In Makira, the occupancy of four out of six native carnivores

was best explained by bird and small mammal relative abundance (Farris *et al.*, 2015b) and a preliminary test using data from Wampole *et al.* (2022) showed native carnivore and “prey” relative abundance were significantly and positively correlated ($R=0.17$, $p<0.001$). In areas where there are few alternate prey present, fosa predation attempts focus on diurnal lemurs (Goodman *et al.*, 1997; Hawkins, 1998), potentially leading to diurnal lemur avoidance of terrestrial foraging. Surprisingly, fosa presence and nocturnal lemur ground use were unrelated, likely due to data small samples sizes, which make it more difficult to understand relationships between covariates and parameters.

Diurnal and nocturnal lemurs were less likely to be observed on the ground within 5 days of a fosa observation. Completely avoiding ground use in areas where fosa are present would be inefficient due to the predator’s wide-ranging activities (maximum home range 224 km²; Wyza *et al.*, 2020), but it is possible to avoid using the ground at locations where fosa have been recently in the short-term. Diurnal lemur spatiotemporal “avoidance” of fosa increased the further a location was from a village or a road. This could be due to a number of factors: an increase in arboreal resources further from human activity (Souza-Alves *et al.*, 2021); an increase in understory that makes it more difficult to be vigilant while foraging on the ground (Barnett *et al.*, 2012a); or an increased likelihood of fosa using the camera location (Rivera *et al.*, 2022). Nocturnal lemur spatiotemporal “avoidance” of fosa increased with increased native carnivore relative abundance. As many nocturnal lemur species are smaller than their diurnal counterparts, they are potential prey to other native carnivores (Goodman, 2003); thus, nocturnal lemurs could perceive camera locations with higher rates of native carnivore activity as too dangerous for terrestriality.

Human presence did not influence lemur ground use, likely due to habituation. Although we were unable to account for it in our analyses, lemur habituation has occurred across Madagascar, particularly in sites selected for ecotourism, and habituation can change the nature and intensity of antipredator behavior in response to humans (LaBarge *et al.*, 2020). Primates studied for longer timespans decrease their ground use (Eppley *et al.*, 2022) and habituated samango monkeys (*Cercopithecus mitis erythrarcus*) perceived terrestrial predation risk to be lower when human observers were nearby (Nowak *et al.*, 2014).

When exotic carnivores were rare, diurnal lemurs used the ground less often at camera locations where humans were present. As dogs were by far our most common exotic carnivore—3,457 observations to 1,116 observations of cats and small Indian civets—we suggest that this result could perhaps be due to more targeted lemur hunting occurring without dogs (Golden, 2009), which could potentially scare off lemurs with their barking. Nocturnal lemurs were more likely to be observed on the ground within 5 days of a human observation but only at camera locations with low native carnivore relative abundance, likely because these camera locations were “safer” for terrestrial foraging due to low native carnivore relative abundance. This positive spatiotemporal association with humans might be due to a spatiotemporal refuge humans created by being present at a location, however brief (Nowak *et al.*, 2014).

In cases where two predators have contrasting spatial distributions or behaviors, prey might exhibit behaviors that indicate choosing the risk of predation by one predator over another (Leblond *et al.*, 2016; Embar *et al.*, 2014). We did not see

an indication of this type of behavior from lemurs spatially; fosa and human relative abundance did not influence the other predator's spatiotemporal relationships with lemurs. This might be due to fosa spatial distribution being little affected by human presence or relative abundance (Farris *et al.*, 2015b; Merson *et al.*, 2019), although fosa do avoid villages and agricultural areas (Rivera *et al.*, 2022; Wyza *et al.*, 2020). However, we did find some indication in diurnal lemur temporal behavior that diurnal lemurs did not perceive humans to be more dangerous than fosa. If diurnal lemurs wanted to avoid using the ground when humans were active—due to perceived predation risk—camera locations where fosa are uncommon would theoretically provide more “safe” hours, particularly around evening, for terrestrial behavior. In such a case, one would expect human-diurnal lemur temporal overlap to decrease at camera locations with low fosa relative abundance. Instead, diurnal lemurs increased ground use, heedless of when humans were active, during early morning hours where fosa were uncommon. However, in the camera locations where fosa are very common, temporal avoidance of them becomes more important; thus, the high early afternoon diurnal lemur activity peak—before fosa become active in the evening—at camera locations where fosa relative abundance is high. These results indicate diurnal lemurs perceive fosa as a more likely or more dangerous predator compared with humans.

Conclusions

Low sample sizes and lack of vigilance data while lemurs were on the ground limits the conclusions drawn from our study of arboreal lemur terrestrial behavior, particularly in response to predator presence. However, we found that fosa presence had more effect on lemur spatiotemporal ground use than human presence and that lemurs take advantage of when and where fosa are uncommon to forage on the ground. This result might be interesting to other researchers; changes in temporal activity depending on the commonness of predators at a survey location could influence data collection. We suggest that researchers consider predator distributions and perceived spatiotemporal predation risk landscapes when deciding when and where to collect observations on lemurs and other primates. As terrestriality in arboreal lemurs, and primates in general, continues and potentially increases, future studies should use a mix of terrestrial camera traps and behavioral observations to better characterize what factors influence when and where lemurs forage on the ground.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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