



# Habitat use and activity patterns of three Eulemur species in the forest and restoration areas of Ranomafana and Ankafobe, Madagascar

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# Habitat use and activity patterns of three Eulemur species in the forest and restoration areas of Ranomafana and Ankafoabe, Madagascar

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## Abstract

Anthropogenic deforestation is a major threat to forest environments, as it leads to habitat loss and fragmentation. Many species suffer from these consequences due to reduced resource availability or connectivity. Forests in Madagascar have drastically been reduced in the past few centuries. There are many projects that focus on forest rehabilitation and restoration but these projects often face challenges. Species-habitat relationships can be specific or spatially variable, and habitat traits that local species require are often not considered in restoration planning. Knowledge on how the species cope with a changing environment is lacking. In Madagascar, frugivorous lemurs can have a large impact on forest regeneration due to their role as seed dispersers, and habitat requirements of these species should be considered in restoration planning. Species of the genus *Eulemur* have shown flexible behavior and potential to cope with environmental changes. In this study, I monitored three *Eulemur* species at two sites in Madagascar; Ranomafana (*E. rubriventer* and *E. rufifrons*) and Ankafobe (*E. fulvus*), which both included forest and restoration areas, as well as a forest fragment at Ankafobe that has recently been burnt. Using arboreal and terrestrial motion sensor camera traps and occupancy modelling, I tested if these species occurred in the disturbed areas. I also compared their locomotion and activity patterns between the habitat types. I tested if they increased terrestrial locomotion as a possible response to reduced connectivity in the disturbed restoration areas, and if they showed a shift in their activity pattern. Due to the less dense vegetation structure in the disturbed areas the lemurs might be more exposed and therefore show a larger proportion of activity at night, possibly to avoid diurnal predators. Although I detected none of the species at the restoration areas, the results suggested that *E. rubriventer* and *E. rufifrons* do occur in the restoration areas, but were not detected due to their small detection probability. These two species used almost exclusively arboreal behavior, with one exception where I detected *E. rufifrons* on the ground. *E. fulvus* does not seem to use the restoration areas at Ankafobe. At Ankafobe the restoration areas were very young and contained a very small number of tree species. These areas therefore seemed to not offer sufficient resource availability for *E. fulvus* to use these areas. *E. fulvus* occurred in the burnt area. There, the species frequently used terrestrial locomotion, but also in the forest, which could be linked to the absence of terrestrial predators or the vegetation structure, as the availability of horizontal branches was limited, and terrestrial locomotion might have been more efficient. All three species showed cathemeral activity in the forest with a peak of activity in the morning and the afternoon, as well as a few detections during the night. *E. fulvus* showed a similar pattern in the burnt area but with a more distributed activity during the day. This could be a response to the decrease in food availability after the fire. Overall, the results suggested that the three species show potential to use disturbed areas and are able to adjust their behavior to changes in the environment, which would be beneficial for forest regeneration due to their role as seed dispersers.

*Keywords:* fragmentation, anthropogenic deforestation, camera traps, occupancy modelling, detection probability

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# 1. Introduction

Many natural environments are affected by anthropogenic disturbances (Fetene et al., 2019). With a growing human population, land conversion is increasing (Danneyrolles et al., 2019), especially in forests (Fetene et al., 2019). Anthropogenic disturbance in forests includes cutting trees, building charcoal pits and plantations, signs of hunting, fire pits or infrastructure, and also leaving trash (Dinsmore et al., 2021a). Deforestation is one of the biggest hazards to forest species (Fetene et al., 2019) since it is often associated with reduced habitat availability and fragmentation (Harper et al., 2007; Kamilar and Tecot, 2016; Dinsmore et al., 2021a). Such disturbances can cause changes in the availability of food and shelter (Aarif et al., 2014; Bryson-Morrison et al., 2017, Finstad et al., 2007), as well as connectivity between resources or habitat patches (Baguette and Van Dyck, 2007), affecting animal behavior and dispersal (Bryson-Morrison et al., 2017; Baguette and Van Dyck, 2007).

Efforts to restore and rehabilitate forests are growing globally (Mansourian et al., 2014; Konersmann et al., 2021), but they face several challenges. Lack of national policies to encourage restoration, education of human populations, as well as high costs and lack of funding (Mansourian et al., 2014) are only a few examples. Species-habitat interactions are complex and often spatially variable (Bradley et al., 2020). For example, koalas (*Phascolarctos cinereus*) have shown different vegetation type requirements in different forests in eastern Australia (McAlpine et al., 2008). Animal-habitat associations that have been studied in one area should not simply be transferred to other areas (Rhodes et al., 2008). Instead, restoration projects should consider habitat-selection cues that the local populations require.

To incorporate habitat-selection cues in restoration, the species using a habitat have to be identified, as well as their diet, food availability requirements throughout the year, and the vegetation structure needed for locomotion and shelter (George and Zack, 2001; Hale et al., 2020). Due to the extensive background knowledge required, these cues are often not considered in restoration planning (Hale et al., 2020).

To restore an ecological community to its original species composition or to restore the ecosystem function of the target habitat, the needs of diverse taxa must be considered. Some taxa prefer or require specific resources of the environment

(Warren, 1997; Warner, 2002; Yu and Lee, 2002; Fuller et al., 2005; Kanowski et al., 2006; Rovero et al., 2014), whereas others are able to adjust their behavioral strategies to cope with environmental variation (Beever et al., 2017; Daniels et al., 2019). Vervet monkeys (*Chlorocebus pygerythrus*), for example, are able to tolerate heat exposure by adjusting their activity. At high temperatures during the non-mating season, this species increases the time spent resting per day while reducing the time spent feeding (McFarland et al., 2014).

Also, the Southern mountain cavy (*Microcavia australis*), a small herbivorous rodent, shows a different diet across sites as a response to the diversity of food available at each site (Sassi et al., 2011). Due to more flexible behavioral repertoires, habitat generalists may be better able to occupy disturbed habitats with sub-optimal vegetation structure or food availability, compared to habitat specialists (Wilson et al., 2008).

Madagascar is a biodiversity hotspot with unique ecosystems due to its high rates of endemism (Myers et al., 2000). However, many ecosystems have been drastically reduced in size and continue to decline (Myers et al., 2000; Ganzhorn et al., 2001). Forests, in particular, are being degraded, reaching a critical state for maintaining biodiversity (Harper et al., 2007). Deforestation is one of the greatest threats to many endemic species (Gade, 1996; Harper et al., 2007; Jones et al., 2019). Between 2001 and 2020, Madagascar's primary forest cover decreased from 4.82 to 3.92 million ha (Mongabay, 2020), a trend that continues (Velo and Zafitsara, 2020). Contributing to this trend is a common land use practice in Madagascar; slash and burn agriculture, or *tavy*, is the cutting and burning of forest or other vegetation to cultivate rice and root crops (Styger et al., 2007). The land is left fallow after the harvest. This practice leads to forest degradation and loss, and often the fire escapes and burns untargeted land (Styger et al., 2007). Knowledge on how species cope with such disturbances and habitat loss is lacking (McLennan et al., 2017).

Forests in Madagascar strongly rely on seed dispersal by endemic frugivorous primates (Dew and Wright, 1998; Ganzhorn et al., 1999; Wright et al., 2011; Albert-Daviaud et al., 2018), many of which are threatened with extinction (IUCN, 2022). For example, Martinez and Razafindratisma (2014) found that the red ruffed lemur (*Varecia rubra*) consumes leaves, fruits or flowers from around 97 plant species in the Masoala National Park and that 90% of all fecal samples they collected, contained at least one seed. Ramananjato et al. (2020) found that two mouse lemur species (*Microcebus rufus* and *M. jollyae*) defecated seeds from 22 different plant species spanning 13 families. These lemurs, and others, contribute to the dispersal of diverse fruiting plant species, benefiting forest regeneration, as several lemur species also increase seed germination and seedling growth after gut passage (Razafindratisma and Razafimahatratra, 2010; Manjaribe et al., 2013; Chen et al., 2016; Ramananjato et al., 2020). This highlights the importance of restoration

projects in Madagascar to include the environmental features required by seed dispersing lemur species, so that they can help to generate a functional ecosystem in restoration areas, as lemurs have also been found to reliably indicate carnivore and rodent species richness in Madagascar's forest ecosystems (Muldoon and Goodman, 2015).

Some lemur species have been found to adjust their diet and/or behavior to environmental changes (Martinez and Razafindratisma, 2014; Kelley et al., 2016; Dinsmore et al., 2021b). The red-bellied lemur (*E. rubriventer*) and the red-fronted lemur (*E. rufifrons*) adjust their behavior with changes in food availability, as both species increase feeding time and decrease time spent travelling in times of food scarcity (Overdorff, 1996). *E. rufifrons* also increases the amount of night activity according to illuminance (Kappeler and Eckert, 2003). Collared brown lemurs (*E. fulvus collaris*) show significant seasonal changes in their day and night activity, as they increase their day activity with longer daylength, but also in disturbed areas (Donati and Borgognini-Tarli, 2006). *Eulemur* species in general show cathemeral activity patterns (Sussman and Tattersall, 1976; Overdorff, 1996; Curtis et al., 1999; Donati et al., 2001; Kappeler and Erkert, 2003; Tarnaud, 2006; Donati et al., 2007; Schwitzer et al., 2007; Sato, 2018). Increased travelling and foraging across exposed branches by *E. rubriventer* have been suggested to correlate with the avoidance of diurnal predators (Overdorff, 1988). The degree of night activity of *Eulemur* species correlates more strongly with environmental variation than with phylogeny, suggesting that this activity pattern might enable these species to flexibly respond to different environmental conditions (Ossi and Kamilar, 2006). Despite such behavioral flexibility, several *Eulemur* species, including *E. rufifrons* and the common brown lemur (*E. fulvus*), are known to avoid dense human settlements, villages and croplands (Kamilar and Tecot, 2016). Further, a study has shown that *E. rubriventer* and *E. rufifrons* prefer taller trees (>15m height), as well as trees with crown diameter greater than 10m (Dagosto and Yamashita, 1998). Therefore, it is unknown if these *Eulemur* species would use restoration areas that lack the vegetation structure of the primary forest, though being amongst the most ecologically flexible lemur species (Ossi and Kamilar, 2006). If they do use restoration areas that have not fully matured, they might increase or be forced to use terrestrial locomotion in areas with smaller trees or large distances between trees. *E. collaris*, for example, has been observed to use terrestrial locomotion to cross open habitat, leaving a small forest fragment possibly to reduce food competition (Donati et al., 2007, 2011).

To assess if these species are able to use disturbed or restoration areas near the forest they inhabit I monitored *Eulemur* species at two different sites in Madagascar; Ranomafana National Park (*E. rubriventer* and *E. rufifrons*) and Ankapobe Reserve (*E. fulvus*). Both sites include primary forest and restoration areas. These two sites therefore offer a good opportunity to determine the



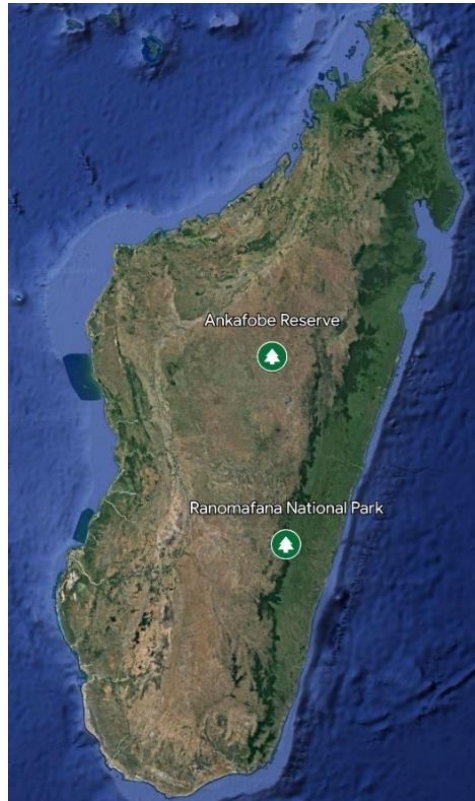
probability of *Eulemur* species using disturbed and/or restoration areas (Q1). If the species did use these areas, I analyzed if they adjusted their behavior. In particular, I analyzed if they moved more terrestrially in these habitat types (Q2), as there might be larger distances between trees compared to the forest. I predicted that this would especially be the case for *E. fulvus*, as the fire in Ankafobe might have reduced connectivity between trees, so they would be forced to move on the ground. Additionally, I looked for shifts in their daily activity pattern to determine if they showed an increase in overall activity level, and if they were more active at night than in the forest (Q3), since they might have increased their activity during the day or at night in the disturbed areas.

## 2. Methods

### 2.1 Study sites and species

Ranomafana National Park (RNP) (Figure 1) is a rainforest park of about 41 000 ha, located in southeastern Madagascar (Wright et al., 2012), including several small reforestation and natural regenerating areas, separated from the forest by an agricultural matrix (Riemann et al., 2015). Since 1989, research has been conducted in RNP. The forest contains thirteen lemur species, including *E. rufifrons* and *E. rubriventer* (Wright et al., 2012). For this project, I used camera trap and vegetation data from the primary forest within RNP, an adjacent restoration area with supported natural regeneration, and actively reforested patches. This data was collected in advance by my collaborators.

Ankafobe Reserve (AR) (Figure 1) is a protected area of about 35 ha, managed by the local community association VOI-Sohisika with the support of Missouri Botanical Garden's (MBG) Madagascar Research and Conservation Program (Andriambeloson et al., 2021). The forest is located within several steep-sided valleys (Andriambeloson et al., 2021). The managed area includes an adjacent restoration area and a few small hilltop restoration areas nearby. Ankafobe Forest hosts three lemur species, including *E. fulvus*.



**Figure 1** Map of Madagascar showing the locations of Ranomafana National Park (21°13'S 47°25'E) and Ankafoabe Reserve (18°7'S 47°12'E). Map created using Google Earth.

On October 6<sup>th</sup> 2022, approximately three weeks before we began the data collection, a grassland fire entered the larger forest fragment at Ankafoabe. The fire burnt about half of the total forest area, including the oldest and largest restoration area (Figure 2). After the fire stopped, local people started collecting the ashes to use them as fertilizer for the native plants. However, invasive plant species, such as *Desmodium uncinatum* (the silverleaf desmodium), immediately started to grow. *Desmodium* can impact terrestrial mobility as this plant has hooked hairs covering its stem (Ravi Kiran et al., 2019), which can trap insects and small mammals. The local people speculated that the fire was started intentionally, as five protected forests in Madagascar were affected by a fire in a single month, including the forest at Ankafoabe.



**Figure 2** Burnt forest fragment at Ankafobe, view from northwest. The edge of the fragment was burnt completely. There were some green patches left in the inner part of the fragment, but the larger part of the forest fragment included partly or completely burnt trees (picture taken on October 23<sup>rd</sup> 2022).

The red-bellied lemur (*E. rubriventer*) occurs in the North of Madagascar and along a stripe of east coast rain forest (IUCN, 2022). This species lives in relatively small pair-bonded groups, consisting of a male, a female and their offspring (Overdorff, 1996). The red-fronted brown lemur (*E. rufifrons*) inhabits forests in the East and West of Madagascar (IUCN, 2022). They usually live in groups of six to ten individuals (Overdorff, 1996), consisting of multiple males and females at their offspring (Pyritz et al., 2011). Changes in group composition or group movements have been observed by leaders of both sexes, however, groups are predominantly led by females (Pyritz et al., 2011). Both of these species occur at Ranomafana. A long-term study showed that the population density changes between *E. rubriventer* and *E. rufifrons* were inverse at Ranomafana, but *E. rufifrons* showed a higher estimated population size and density (Wright et al., 2012). *E. rubriventer* seems to be more specialized than *E. rufifrons* concerning diet (Razafindratsima et al., 2014). The common brown lemur (*E. fulvus*) occurs in the North and the East of Madagascar (IUCN, 2022), and lives in multi-male, multi-female groups of three to twelve individuals (Jacobs et al., 2008; Mittelmeier et al., 2010; Tonnabel et al., 2011). This species inhabits the forest at Ankafobe. All three species are important seed dispersers, feeding on fruits from several different plant species and families (Dew and Wright, 1998; Sato, 2013).

## 2.2 Data collection

We collected the data at Ranomafana from February to June 2022, and at Ankafobe from October to December 2022. We used camera traps to detect the *Eulemur* species present at these sites. Additionally, we conducted vegetation sampling to include habitat characteristics in our analysis that might affect the detection or occupancy probability of the species.

### 2.2.1 Camera traps

Using arboreal camera traps instead of line-transect surveys, or in addition to terrestrial camera traps, seems to improve monitoring of arboreal species (Gregory et al., 2014; Bowler et al., 2017; Moore et al., 2021). We used Reconyx Hyperfire 2 trail cameras with motion sensors and infrared night images and set the camera to take three images with 1s time interval when triggered, following a 30 s time interval before the camera could be triggered again. The deployment points, location of paired arboreal and terrestrial cameras (arboreal and terrestrial deployment), were placed at a density no greater than two per ha, a minimum of 0.25 km from the edge of the habitat type (forest, restoration or burnt) and 0.5 to 1 km from another deployment point. For Ranomafana forest, we randomly selected ten points from an existing terrestrial camera trap grid and placed cameras on those points, as well as a deployment point 0.5 to 1 km away. All other habitat patches at both sites were too small to use a grid, so we aimed to reach 20 deployment points, or as many as possible, per habitat type. A deployment point was located at a tree with a horizontal branch where the arboreal camera could aim towards, or where the camera could aim at an adjacent tree, and a tree fork higher above the suitable branch for the rope we used to climb the tree according to a stationary rope system (SRS) tree climbing technique. We deployed the arboreal cameras at 10 to 20 m height, depending on the height of the tree and the suitable branch, as well as the canopy height.

The terrestrial camera traps we deployed at 0.5 m height, aiming towards an area we cleared of grass that could trigger the motion sensor of the camera. The height of the terrestrial cameras was the only standardized variable. We set the angle of the terrestrial camera depending on the steepness around the deployment tree, and that the camera aimed along the ground where the vegetation least restricted the view of the camera.

At Ankafobe, we established a total of 34 deployment points, 14 in the forest, 10 in the restoration areas, and 10 in the forest fragment that was affected by the fire. In Ranomafana, we established a total of 42 deployment points, 20 in the forest, and 22 in restoration areas (Table 1). Following Chen et al. (2021), we deployed paired

ground and arboreal camera traps on the same tree (deployment point), where possible. If the trees in an area were not tall enough or did not provide sufficient structure, we omitted the arboreal cameras (Table 1).

The cameras were active around 40 days at Ankafobe and around 60 days at Ranomafana. The number of camera trap days at Ranomafana was predefined, as this project was part of a larger study. The smaller number of camera trap days at Ankafobe was due to organizational limitations. We tried to keep the cameras active as long as possible. For some cameras we checked the batteries and SD cards in between, for which we had to turn them off. If we turned off the cameras during the trapping period, we considered it a new deployment (arboreal or terrestrial camera of a deployment point) when we turned them back on (later referred to as deployment number; D1 or D2), as the camera angle was sometimes adjusted and our presence at the cameras might have disturbed the animals (Bornbusch and Drea, 2021). This affected 28 deployment points at Ranomafana; six in the forest and all in the restoration areas, none at Ankafobe. At these deployment points we turned off both the arboreal and the terrestrial cameras (Table 1).

*Table 1* Number of arboreal and terrestrial cameras/deployments, total number of deployment points, additional deployments (D2) due to turning off the cameras during the collection period, and number of deployments (total of all arboreal, terrestrial cameras, as well as deployments D1 and D2) per site and habitat type.

	Ranomafana		Ankafobe		
	Forest	Restoration	Forest	Restoration	Burnt
Arboreal cameras (arboreal deployment)	20	22	14	1	10
Terrestrial cameras (terrestrial deployment)	20	22	14	10	10
Total deployment points (paired arboreal and terrestrial deployment)	20	22	14	10	10
Additional deployments (D2)	12	22	0	0	0
Total deployments (arb, ter, D1, D2)	52	88	28	11	20

I classified the images, identifying all animals to the species level if possible and consulted my collaborator M. A. in case of uncertainty. Due to the fact that the camera made three consecutive images when triggered, I focused on the independent photo events, which I defined as all images of the same species that were captured by a camera at least 30 minutes apart, following Chen et al. (2021). Therefore, if an individual was spending quite some time in front of the camera, it only counted as one independent event. This included other cameras, as several deployment points were located in a single *Eulemur* home range, which led to one exclusion of a photo event in the burnt area at Ankafobe.

### 2.2.2 Vegetation sampling

For each deployment point tree, we measured several characteristics to determine which features were associated with the presence or absence of the three *Eulemur* species, as well as factors that could affect the detection of the lemurs by the cameras. These characteristics included tree height, tree species, tree DBH (diameter at breast height), tree crown height, tree crown diameter, tree crown shape, amount of flowering and young leaves (percentage), amount of ripe and unripe fruits (percentage), camera direction (N, NE, E, SE, S, SW, W, NW), branch length and diameter (only for arboreal cameras). Further, we measured the canopy cover (yes, no) and ground cover type (dead leaves, vegetation, wood, soil, water, rock) every 1m for 25 m in each cardinal direction around the deployment tree, using a GRS densitometer to measure both variables. The ground cover types I then collapsed to ground composition that could reduce detectability in front of the camera (percentage of vegetation, rock, wood). We also noted all tree species (incl. DBH, height, crown height, crown diameter and shape) in the 5 m radius around the deployment tree. The visibility of the terrestrial cameras at Ankafobe we estimated using poles which we put in front of the camera at 2 m, 4 m and 6 m distance, which we removed again after triggering the camera. For the purpose of the analysis, I defined the visibility as a number between 0 and 2 depending on how many poles were visible on the camera image.

## 2.3 Statistical analysis

### 2.3.1 Use of different habitats

I conducted single-season, single-species occupancy models for each species in R version 4.2.0, using the unmarked package (Fiske and Chandler, 2011). Occupancy refers to the probability of a species inhabiting a particular location within a designated area, while accounting for imperfect detection (MacKenzie et al., 2003). Occupancy modeling has already shown potential for monitoring primate populations (Keane et al., 2012; Campbell et al., 2019; Chen et al., 2021). As we installed multiple deployment points in a single *Eulemur* home range, I interpreted the results rather as “probability of use” instead of occupancy (MacKenzie and Royle, 2005).

Since none of the species occurred at both study sites, I conducted separate models for each species. Further, I also conducted separate models for the arboreal and terrestrial cameras to be able to include different detection covariates, as different factors might have influenced the detectability depending on the location of the camera (arboreal or terrestrial).

My original models showed that many vegetation variables were highly correlated ( $r > 0.7$ ) with habitat type, so I excluded them from further analysis. For the arboreal models I then included camera direction, branch length and branch diameter, as well as the combination of camera direction with either branch length or branch diameter. For the terrestrial cameras, I included camera direction, ground composition and visibility, as well as combinations of these variables. I set the occupancy as constant to test which probability of detection model could explain the data best using the Akaike Information Criterion (AIC). Then I used the model with the lowest AIC, as well as all models with an AIC of less than two units difference from the lowest, and included habitat type as occupancy covariate. For the models of *E. rubriventer* and *E. rufifrons*, I also included deployment number (D1 or D2) as occupancy covariate. For the detections, I created separate files for each species, as well as the arboreal and terrestrial data of *E. fulvus*. I collapsed every three days into a single sampling occasion (Chen et al., 2021), using presence/absence (0,1) data per sampling occasion and camera.



### 2.3.2 Arboreality

I calculated the total capture rate (number of photo events per number of trap days) for each species and the capture rate per habitat type, as well as the capture rate per camera location (arboreal or terrestrial) to elaborate if there was a difference in the proportion that each species spent on the ground between the habitat types. Also, I compared the occupancy probabilities of the arboreal and the terrestrial models to answer this question.

### 2.3.3 Activity pattern

To test if the three *Eulemur* species showed a shift in the proportion of their day and night activity across habitat types, I calculated the day and night capture rate for each species and each habitat type. Further, I plotted the proportion of images per time of day to see if they showed cathemeral activity patterns in the forest, as well as in the other habitat types and I compared the activity distribution and the times of peak activity over a 24 h cycle between habitat types.

### 3. Results

Some cameras stopped recording after a few weeks as the storage capacity was reached. Due to wind, the arboreal cameras got triggered a lot by moving branches. Two terrestrial cameras in the burnt area at Ankafobe were stolen, as well as two arboreal and two terrestrial cameras at Ranomafana, leaving 80 cameras at Ranomafana and 57 at Ankafobe. From the remaining 137 cameras we captured 648 711 images, 1 341 of which contained one of the three *Eulemur* species (Figure 3). Of these, 150 were independent photo events. Less than ten lemur images were not identifiable, as only part of the animal was visible in the image.

At six of 80 cameras at Ranomafana we detected *E. rubriventer* (Figure 4), while we detected *E. rufifrons* at nine cameras (Figure 5), resulting in 13 independent photo events of *E. rubriventer* and 45 of *E. rufifrons* (Table 2 and 3). One of the photo events of *E. rufifrons* was captured by a terrestrial camera, which was the only terrestrial *Eulemur* photo event at Ranomafana. All detections of *E. rubriventer* and *E. rufifrons* were captured by cameras in the forest, none by the cameras in the restoration areas.

There was one arboreal nighttime photo event at Ranomafana in the restoration area that was most likely a *Eulemur*. However, three independent observers were unable to identify the photo event to the species level. I therefore excluded this event from the analysis. The image was taken in the restoration area closest to the forest, which was a natural regeneration area.

At Ankafobe, we detected *E. fulvus* at 31 of 57 cameras (Figure 6), resulting in 92 independent photo events. Of these, 29 photo events were captured by terrestrial cameras (Table 2 and 3). Also for this species none of the detections were captured by cameras in the restoration areas. However, 39 of the arboreal and 18 of terrestrial photo events we captured with cameras in the burnt area, which both are larger numbers than the number of photo events in the forest.



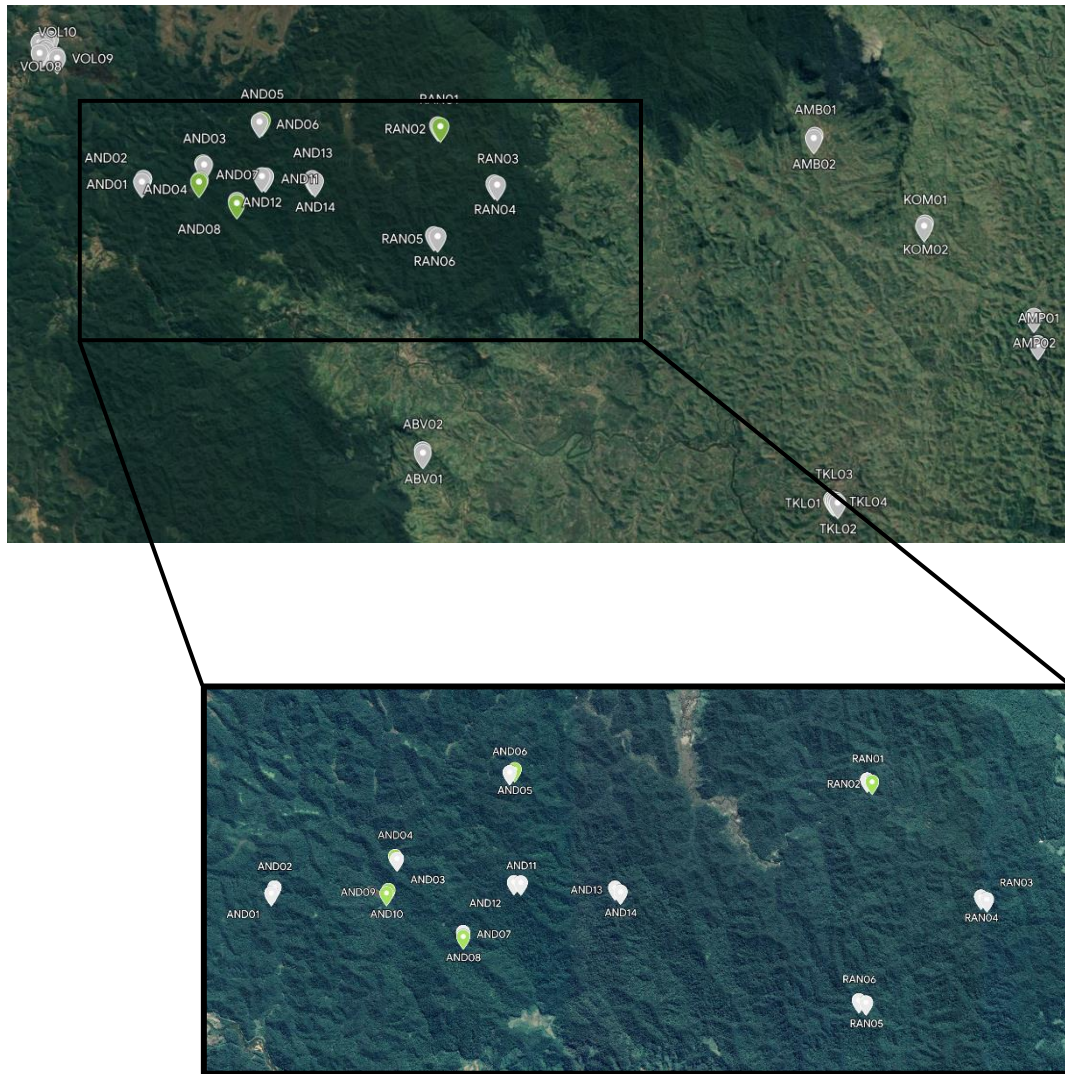
**Figure 3** Examples of detections from the three study species. From top left to bottom right; arboreal *E. rubriventer* (male), arboreal *E. rufifrons* (one female, two males), arboreal *E. fulvus* (male), terrestrial group of four *E. fulvus*.

**Table 2** Total number of cameras that could detect each species (stolen cameras excluded), number of cameras with detections, number of images and photo events for all three study species.

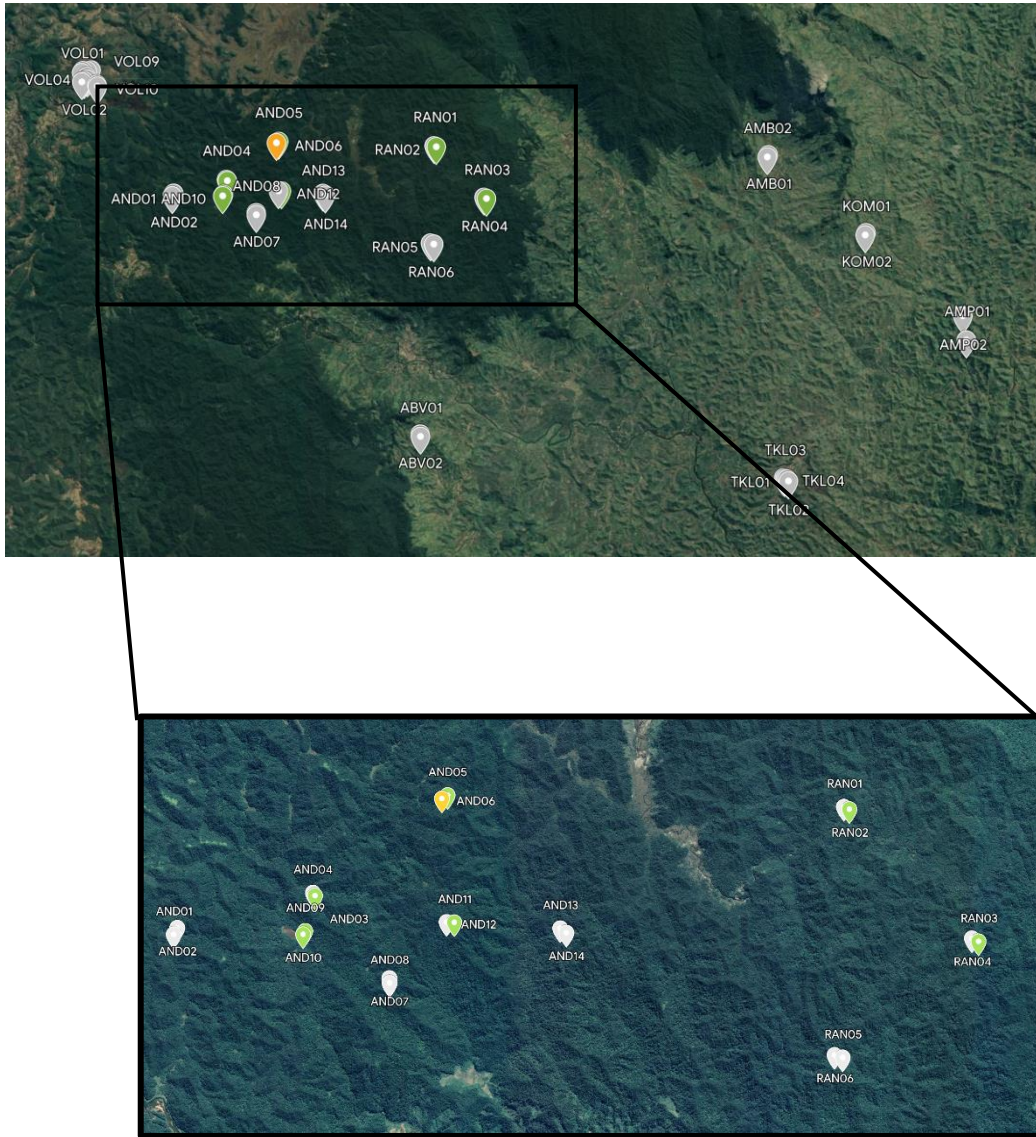
Species	Total number of cameras	Number of cameras with detections	Total number of images	Total number of photo events
<i>E. rubriventer</i>	80	6	43	13
<i>E. rufifrons</i>	80	9	779	45
<i>E. fulvus</i>	57	31	519	92

**Table 3** Number of photo events of each of the three study species and for each habitat type (forest, restoration, burnt) and camera location (arboreal, terrestrial).

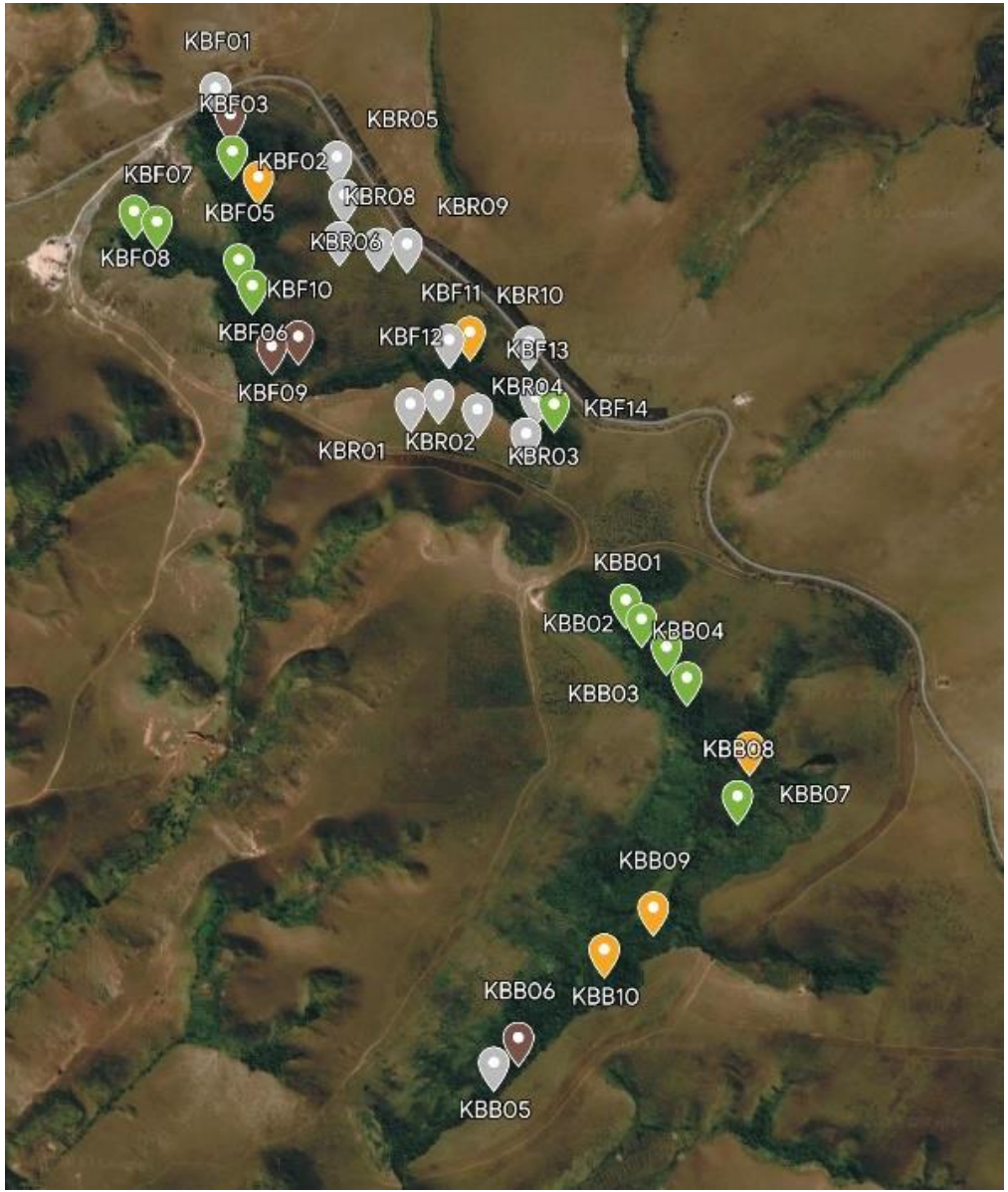
Species	Forest		Restoration		Burnt	
	arboreal	terrestrial	arboreal	terrestrial	arboreal	terrestrial
<i>E. rubriventer</i>	13	0	0	0	-	-
<i>E. rufifrons</i>	44	1	0	0	-	-
<i>E. fulvus</i>	28	11	0	0	35	18



**Figure 4** Deployment points at Ranomafana for *E. rubriventer*; Ambatovy (ABV), Ampitambe (AMB), Andrannofady (AND), Kianjanomby (KOM), Ranomena (RAN), Tanambao kelilalina (TKL), Voloero (VOL); AND and RAN in the forest; VOL in natural regeneration; ABV, AMB, AMP, KOM and TKL reforestation. Colors show detections; none (grey), arboreal (green), terrestrial (brown), both arboreal and terrestrial (orange).



**Figure 5** Deployment points at Ranomafana for *E. rufifrons*; Ambatovy (ABV), Ampitambe (AMB), Andrannofady (AND), Kianjanomby (KOM), Ranomena (RAN), Tanambao kelilalina (TKL), Voloero (VOL); AND and RAN in the forest; VOL in natural regeneration; ABV, AMB, AMP, KOM and TKL reforestation. Colors show detections; none (grey), arboreal (green), terrestrial (brown), both arboreal and terrestrial (orange).



**Figure 6** Deployment points at Ankafobe (KB) for *E. fulvus*; KBF forest, KBR restoration, KBB burnt area. Colors show detections; grey none, green arboreal, brown terrestrial, orange both arboreal and terrestrial.

## 3.1 Habitat use

### 3.1.1 Detection

I conducted arboreal occupancy models for all three species; however, due to sample size restrictions I was only able to conduct a terrestrial model for *E. fulvus*. For all three species, arboreal models including either branch length or branch diameter as detection covariate explained the data best, while the combination of ground composition and visibility performed best as detection covariates for the terrestrial model of *E. fulvus* (Appendix 1). However, branch length showed a significant influence on detection probability only for *E. fulvus* (estimate = 0.402,  $p = 0.004$ ) in the arboreal models. For the other two species, the detection covariates were not significant, and the estimates did not show a strong relationship (*E. rubriventer* estimate = 0.206; *E. rufifrons* estimate = 0.074). For the terrestrial model of *E. fulvus*, visibility showed a significant influence on detection probability (estimate = 1,  $p = 0.02$ ), ground composition did not but the estimate showed a negative relationship between ground composition and detection probability (estimate = -1.25) (Appendix 1). The other detection covariates showed a positive relationship with detection probability.

Average detection probability ranged from 0.05 to 0.172 in the forest, with the highest detection probability for *E. rufifrons* and the lowest for *E. rubriventer*. We detected *E. rufifrons* more than three times as often as *E. rubriventer* (Table 2 and 3). The detection values were lower in the restoration areas for all species. For *E. fulvus*, the arboreal model showed a higher detection probability than the terrestrial model for all habitat types. The arboreal detection probability of *E. fulvus* was higher in the burnt area than in the forest (Table 4).

### 3.1.2 Occupancy

General patterns of occupancy were consistent between the two deployment numbers (D1 and D2) for the cameras we turned off during the data collection period at Ranomafana. For all three species, occupancy probability was higher in the forest than in the restoration areas, with *E. fulvus* showing the largest difference between habitat types, in both the arboreal and the terrestrial model. The arboreal occupancy probability of *E. fulvus* in the burnt area was higher than in the forest (Table 4). There were large differences between deployment points in a habitat type.

**Table 4** Arboreal occupancy models with lowest Akaike Information Criterion (AIC) for each species, and terrestrial occupancy model for *E. fulvus*; showing the detection covariates  $p$  and occupancy covariates  $\psi$ , as well as average detection probability and occupancy probability for each habitat type and deployment (D1 or D2 for species at Ranomafana).

Species	Model	AIC	Average detection (SE)	Occupancy (SE)	Habitat
<i>E. rubriventer</i> arboreal	p(branch_len), $\psi$ (habitat_type + deployment_nr)	109.7261	0.050 ± 0.028	0.435 ± 0.264	forest D1
			0.062 ± 0.034	0.355 ± 0.229	forest D2
			0.031 ± 0.025	0.145 ± 0.186	restoration D1
			0.031 ± 0.025	0.108 ± 0.139	restoration D2
<i>E. rufifrons</i> arboreal	p(branch_diameter), $\psi$ (habitat_type + deployment_nr)	189.129	0.143 ± 0.044	0.285 ± 0.120	forest D1
			0.172 ± 0.054	0.342 ± 0.175	forest D2
			0.087 ± 0.051	0.108 ± 0.094	restoration D1
			0.087 ± 0.051	0.136 ± 0.116	restoration D2
<i>E. fulvus</i> arboreal	p(branch_len), $\psi$ (habitat_type)	228.5609	0.127 ± 0.031	0.841 ± 0.194	forest
			0.081 ± 0.030	0.001 ± 0.032	restoration
			0.203 ± 0.042	0.995 ± 0.102	burnt
<i>E. fulvus</i> terrestrial	p(ground_composition + visibility), $\psi$ (habitat_type)	173.0833	0.073 ± 0.024	1.000 ± 0.002	forest
			0.054 ± 0.039	0.000 ± 0.001	restoration
			0.088 ± 0.029	1.000 ± 0.005	burnt



## 3.2 Arboreality

Both species at Ranomafana, *E. rubriventer* and *E. rufifrons*, showed higher capture rates for the arboreal data compared to the terrestrial data, with no captures of *E. rubriventer* on the terrestrial cameras and only one of *E. rufifrons* (Table 5). For *E. fulvus* at Ankafoke, I calculated an arboreal capture rate (number of detections per total number of camera trap days) of 0.065 and a terrestrial capture rate of 0.023 (Table 5).

**Table 5** Total number of camera trap days (all cameras combined), total number of photo events for each habitat type and camera location (arboreal, terrestrial,) and capture rate (number of photo events per total number of trap days) for each of the three study species.

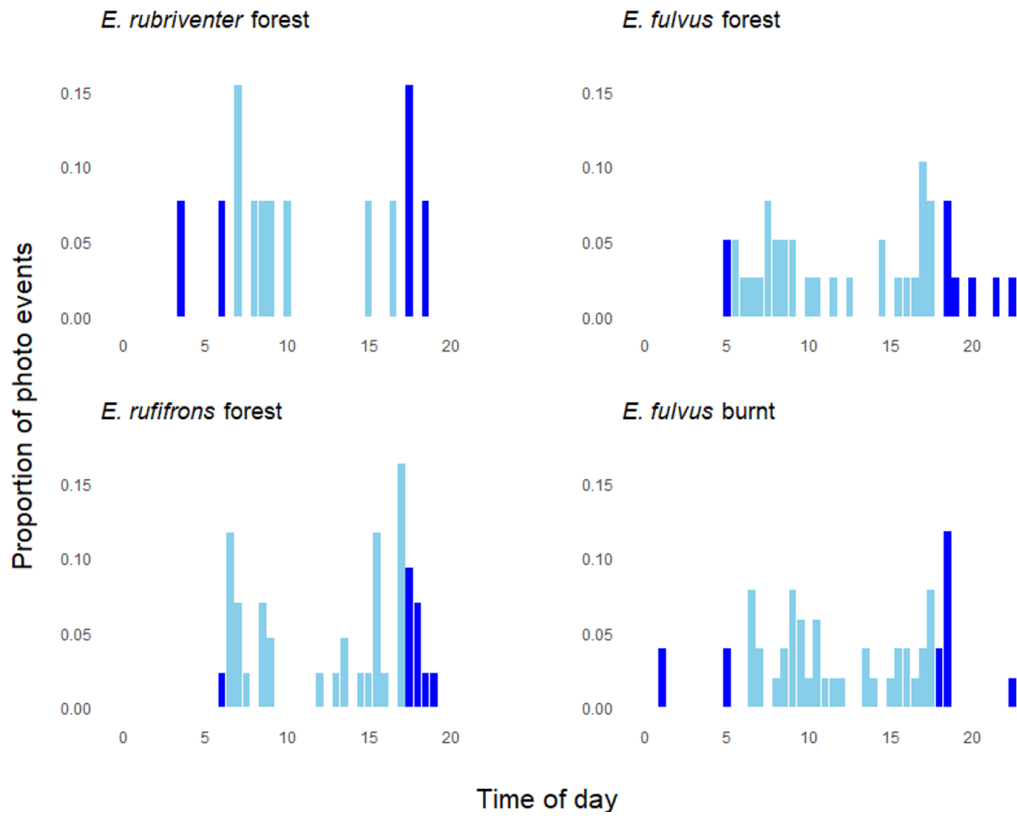
	<i>E. rubriventer</i>			<i>E. rufifrons</i>			<i>E. fulvus</i>		
	Trap days	Detections	Capture rate	Trap days	Detections	Capture rate	Trap days	Detections	Capture rate
Burnt	-	-	-	-	-	-	1112	39	0.035
Forest	2260	13	0.006	2260	45	0.020	703	53	0.075
Restoration	3000	0	0	3000	0	0	404	0	0
<b>Total</b>	<b>5260</b>	<b>13</b>	<b>0.002</b>	<b>5260</b>	<b>45</b>	<b>0.009</b>	<b>2219</b>	<b>92</b>	<b>0.042</b>
Arboreal burnt	-	-	-	-	-	-	556	28	0.050
Arboreal forest	1131	13	0.012	1131	44	0.039	389	35	0.090
Arboreal restoration	1470	0	0	1470	0	0	21	0	0
<b>Total arboreal</b>	<b>2601</b>	<b>13</b>	<b>0.005</b>	<b>2601</b>	<b>44</b>	<b>0.017</b>	<b>966</b>	<b>63</b>	<b>0.065</b>
Terrestrial burnt	-	-	-	-	-	-	556	11	0.020
Terrestrial forest	1129	0	0	1129	1	0.001	314	18	0.057
Terrestrial restoration	1530	0	0	1530	0	0	383	0	0
<b>Total terrestrial</b>	<b>2659</b>	<b>0</b>	<b>0</b>	<b>2659</b>	<b>1</b>	<b>0.000</b>	<b>1253</b>	<b>29</b>	<b>0.023</b>

### 3.3 Activity pattern

All three species showed a similar proportion of day/night activity (Table 6), and a similar activity pattern with a peak between dawn and 9 a.m. and a peak around sunset. We detected all species primarily during the day, but also quite a few times before sunrise or after sunset, with a few detections of *E. fulvus* in the middle of the night in both the forest and the burnt area (Figure 7').

**Table 6** Proportion of activity during the day vs at night for each species in the forest, as well as in the burnt area for *E. fulvus*. Day and night were defined according to sunrise and sunset. For *E. rubriventer* and *E. rufifrons* sunrise was around 5.30 a.m. and sunset around 6.00 p.m., for *E. fulvus* sunrise was around 5 a.m. and sunset around 6.30 p.m. depending on the months of data collection.

Species	Proportion of activity day vs. night
<i>E. rubriventer</i> (forest)	0.615
<i>E. rufifrons</i> (forest)	0.767
<i>E. fulvus</i> (forest)	0.769
<i>E. fulvus</i> (burnt)	0.745



**Figure 7** Proportion of photo events per time of day over the 24 h cycle, rounded to the nearest half hour for *E. rubriventer*, *E. rufifrons* and *E. fulvus* in the forest, and for *E. fulvus* in the burnt area. Colors represent day (light blue) and night (dark blue). Day and night were defined according to sunrise and sunset. For *E. rubriventer* and *E. rufifrons* sunrise was around 5.30 a.m. and sunset around 6.00 p.m., for *E. fulvus* sunrise was around 5 a.m. and sunset around 6.30 p.m. depending on the months of data collection.

## 4. Discussion

### 4.1 Detection

The detection covariates for the arboreal models varied little between the species in this study. For *E. rufifrons*, I found a positive relationship between detection probability and branch diameter, which is consistent with a study discovering that the choice of support (or branch) on which a lemur moves is influenced by angle and diameter of this support (Gebo, 1987). *E. rufifrons* has shown to preferably use branches with diameter between 2.5 and 10cm at Ranomafana (Dagosto and Yamashita, 1998). I found a positive relationship between detection probability and branch length for *E. rubriventer*, as well as for *E. fulvus*. A longer branch increases the field of view in front of the camera and could therefore increase detection probability. The detection probability of *E. fulvus* in the burnt area was higher than in the forest, most likely because there were many openings in the vegetation structure due to the fire. Visibility has been shown to increase in less dense vegetation (Hofmeester et al., 2017).

### 4.2 Occupancy

The three species showed a difference in occupancy, mainly between the two sites. *E. rubriventer* and *E. rufifrons* show an occupancy probability around 30-45% in the forest, whereas *E. fulvus* shows a much higher occupancy probability of 85% in the forest. This could be influenced by the size of the forest fragments and the smaller distance between the cameras, as the forest corridor in Ranomafana is significantly larger than the remnant forest at Ankafobe. Therefore *E. fulvus* could be seen on several cameras, influencing the overall occupancy probability in the forest. *E. fulvus* showed an even higher occupancy probability in the burnt area compared to the forest. This is most likely because the individuals in the burnt area had to increase foraging in the remaining green forest patches due to the drastic decrease of habitat and resources.

The forest fragment in Ankafobe, as well as the fragment that was affected by the fire, were smaller than the published home range of *E. fulvus* (Sato, 2013). This

could lead to crowding of *E. fulvus* populations at Ankafobe. Forest loss and fragmentation has been shown to promote crowding in several species (Schmiegelow et al., 1997; Gestich et al., 2022), including lemurs (Gabriel et al., 2018), which can result in aggressive behavior and intraspecific food competition (Nieuwenhuijsen and De Waal, 1982; Armario et al., 1984; Gabriel et al., 2018). Crowding after the massive habitat loss due to the fire could lead to an eventual reduction of the *E. fulvus* population or even to the species extinction at Ankafobe, as a result of insufficient resource availability (Holt et al., 2005). To analyze this, the *E. fulvus* population at Ankafobe should be further monitored, including the species richness, which we did not focus on in this study.

Despite higher overall detection of *E. rufifrons* in the forest, I found a lower occupancy probability in the forest for this species compared to *E. rubriventer*. A possible explanation for this could be that *E. rufifrons* shows much more backtracking behavior, reversal of movement ( $\pm 180^\circ$ ), compared to *E. rubriventer* (Razafindratsima et al., 2014). *E. rufifrons* has also been reported to often return to a tree with high preferred food density the same day or a few days later (Erhart and Overdorff, 2008), which we also observed as most detections of *E. rufifrons* occurred at the same deployment point. This could be due to their relatively large group size (Razafindratsima et al., 2014), as they need a larger amount of food to saturate all individuals and would return to a tree that offers a large food availability. A study on movement and seed dispersal by these two species has shown that *E. rubriventer* dispersed seeds significantly further away from the parent trees compared to *E. rufifrons* (Razafindratsima et al., 2014). The occupancy model calculated the overall occupancy probability of the forest and not the probability per deployment point, therefore the overall occupancy probability is smaller when the species mainly occur at one or two deployment points, compared to when the species occurs at several different deployment points.

The two species at Ranomafana show a higher occupancy probability in the restoration areas compared to *E. fulvus* at Ankafobe, even though we did not detect any of the three species in this habitat type. The restoration patches at Ankafobe were quite young (less than 8 years old) and we found hardly any trees large enough to install an arboreal camera. The small number of arboreal cameras in this habitat type affects the detection probability (Pease et al., 2016), but also highlights the long process of restoration. Also, due to a funding restriction for the restoration project at Ankafobe, the number of tree species in the restoration areas was restricted to less than ten different species. In the Ankarafantsika National Park in northwestern Madagascar, seeds of 70 plant species have been found in faeces of *E. fulvus* throughout a year (Sato, 2013). Given this dietary diversity of *E. fulvus*, the limited tree species diversity in the restoration areas at Ankafobe could be an important factor on why this species would not use these areas.

In Ranomafana, the restoration patches were quite diverse concerning habitat characteristics such as canopy cover, tree height and species diversity, but overall, the restoration areas and the forest at Ranomafana show more similarities than the different habitat types at Ankafobe. As the occupancy model accounts for imperfect detection (MacKenzie et al., 2003) the results showed an occupancy probability larger than zero, although we did not detect either species. The occupancy probability was around 10-15% for *E. rubriventer* and *E. rufifrons*. The detection probability was very low; therefore the occupancy model suggests that, according to the detection data, *E. rubriventer* and *E. rufifrons* could occur in this habitat type, but were simply not detected by our camera traps. This is an important result as the occurrence of these species could have a positive effect on vegetation regeneration in the restoration areas at Ranomafana due to their role as seed dispersers (Dew and Wright, 1998; Razafindratsima and Dunham, 2015).

However, these results were site specific and there was a large variation between deployment points in the same habitat type, especially in the restoration areas. To get more insight on which specific habitat traits influence the occurrence of these *Eulemur* species, further research needs to be conducted. Also, to test the influence of the distance of the restoration areas to the forest, as a matrix can have an influence on the dispersal of animals (Fahrig, 2007).

### 4.3 Arboreality

Most lemur species show a mainly arboreal locomotion (Ashton and Oxnard, 1964). The only lemur species to prefer terrestrial locomotion is the ring-tailed lemur (*Lemur catta*) (Gebo, 1987). *E. rubriventer* and *E. rufifrons* use leaping or quadrupedalism along horizontal branches most frequently (Dagosto and Yamashita, 1998). Both species have previously been reported on the ground; however, very rarely (Tilden, 1990; Amoroso et al., 2020). A study on the effect of water scarcity on *E. rufifrons* showed that most long-distance displacements of this species occurred on the ground (Scholz and Kappeler, 2004). Further, *E. rufifrons* has been observed to visit artificial waterholes on the ground as a response to scarce water availability (Amoroso et al., 2020), supporting the potential of this species to adjust its behavior to environmental conditions, even though we did not capture them with our ground cameras. The detection rate of these two species was relatively small even in the forest. This could be the reason we did not detect them on the ground as there the detection rate would be even smaller if they usually use arboreal locomotion. However, these species might not need to move on the ground as the vegetation structure in the forest offers sufficient support to move arboreally. The larger number of detections with terrestrial cameras for *E. fulvus* compared to *E. rubriventer* and *E. rufifrons* could be due to a lack of terrestrial predators at Ankafobe. The lemurs at Ankafobe are more used to human presence as local people and the staff from the reserve at Ankafobe regularly use paths through the forest. This could have reduced their perception of threat from human presence. Also, during our stay at Ankafobe we observed people feeding the lemurs and one lemur group also repeatedly visited the camp and fed on fruits or food leftovers in the provided campsite trash receptacle. The high proportion of time they spent on the ground could be an adjustment of these factors at Ankafobe. However, as we were establishing the deployment points, we sometimes had a hard time finding a tree with a horizontal branch, which could make arboreal locomotion more challenging for the lemurs. The vegetation structure of the forest could therefore also be a factor on why this species was often detected on the ground, as this type of locomotion might be more efficient. This would support the possibility that this species shows behavioral flexibility and is able to cope with human disturbance. A study on the behavior of captive crowned lemurs (*Eulemur coronatus*) has shown that the lemurs increased interactions with visitors over time as they do visitor feeds in the zoo they live in (Jones et al., 2016), which suggests that the lemurs make a connection of human presence and food availability.

Despite showing a lower capture rate on the terrestrial cameras compared to the arboreal ones, the models calculated a slightly higher occupancy probability of *E. fulvus* on the ground than in the trees. The detection probability was smaller for the

terrestrial cameras and the models might therefore assume, that the species occurred on the ground more frequently than we were able to detect.

In Ankafobe, the capture rate of *E. fulvus* was smaller for the ground cameras in the forest than the ones in the burnt area. The fire reduced connectivity between trees due to burnt branches and a reduction of tree density, therefore the lemurs might have had to adjust their locomotion to reach intact trees. This is supported by a study on two orangutan species (*Pongo abelii* and *P. pygmaeus*) that has shown that the locomotion of these primate species is influenced by forest structure and support availability (Manduell et al., 2012). Further, *P. pygmaeus* has shown to increase terrestrial movement in areas with higher burning intensity in Borneo (Widyastuti et al., 2022).

#### 4.4 Activity

The three species in this study have all shown cathemeral behavior. They showed activity at day and at night with a peak in the morning, as well as in the afternoon. This pattern has also been described for the collared brown lemur (*E. collaris*) (Donati et al., 2016). The activity of *E. collaris* has been observed in forest fragments with different degrees of disturbance and the species showed increased nocturnal activity in the more disturbed fragments (Donati et al., 2016). Cathemeral behavior has many advantages and allows *Eulemur* species. to flexibly respond to changes in their environment (Wright, 1999). By adjusting the activity pattern, interspecific feeding competition can be reduced, as well as predation risk (Tattersall, 2008). Further, cathemeral species can adjust the amount of time feeding in times of food scarcity or reduced food quality due to seasonal changes (Tarnaud, 2006; Tattersall, 2008), or as a thermoregulatory mechanism (Curtis et al., 1999). The activity pattern of *E. fulvus* in the forest and the burnt fragment are quite similar, but their activity is slightly more spread throughout both day and night in the burnt area, which suggests more foraging periods in an area where resources are scarce (Tattersall, 2008). However, further research should be conducted to support this hypothesis.



## 4.5 Limitations

To make stronger statements about the occupancy of lemur species, the monitoring should be conducted during different seasons to differentiate between changes in the species behavior as a response to seasonal changes in the environment compared to adjustments to the different habitat types. The sample size was limited due to the small area at Ankafobe, as well as the age and the number of restoration areas at both sites. With a larger sample size, a separate analysis of the different deployment points in a habitat type could have been conducted, as there were large differences between deployment points. However, this is the current situation in most areas in Madagascar and it is still important to monitor disturbed and restoration areas and look at early patterns of use, especially by frugivorous lemurs which can promote restoration as their role as seed dispersers (Dew and Wright, 1998; Ganzhorn et al., 1999; Wright et al., 2011; Albert-Daviaud et al., 2018).

Due to a lot of wind, the arboreal cameras were often triggered by moving branches, which resulted in thousands of images without an animal. The process of image classification was therefore very time consuming. Also, some of the batteries ran out before we took down the cameras. This could be improved by changing the batteries more frequently in the arboreal cameras and in the future AI could be used to assist in classifying the images.

The variables I initially included in the models correlated with the habitat type and I had to exclude them from the analysis. This led to sparse models for the probability of detection. Additional variables should be measured in future projects to elaborate more precisely which factors could influence the detection probability of these species.

All three *Eulemur* species only inhabit one of the two sites, so I was not able to compare them. Some differences between the species could therefore also emerge from site differences. To better understand the behavioral flexibility and difference between the species, they should be monitored at additional locations with varying forest size and degree of disturbance. This would give more insight on which behaviors are species-specific and which are due to environmental conditions.

## 4.6 Conclusion

Monitoring local species can help understand how these species cope with anthropogenic disturbance and habitat loss. It is especially important, that habitat traits required by seed dispersing mammals are included in restoration projects, as these species can help promoting plant communities and ecosystem function (Albert-Daviaud et al., 2018). The results of this study suggest that *E. rubriventer* and *E. rufifrons* show potential to occur in restoration areas at Ranomafana. Due to their cathemeral activity pattern and their ability to move terrestrially (Scholz and Kappeler, 2004; Amoroso et al., 2020), *Eulemur* species can adjust their behavior to environmental changes or habitats with sub-optimal vegetation traits. *E. fulvus* at Ankafobe also appeared to cope with recent disturbances, as the species showed more activity distributed during the day in the burnt area. Also, *E. fulvus* used more terrestrial locomotion in the area that was affected by the fire. The species showed low probability to occur in the restoration areas at Ankafobe; however, these areas do not yet offer enough shelter and food availability due to the young age of the planted trees and the low diversity of tree species. It is important that all three lemur species continue to be monitored at these sites as all show potential to use disturbed areas and monitoring could give insight into what habitat traits they require. As seed dispersers, these *Eulemur* species could have a large impact on forest rehabilitation and regeneration and their occurrence in restoration areas could also assist in the survival of other species in an era of rapid habitat reduction and destruction.

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## Popular science summary

Three lemur species show potential to use disturbed or restoration areas in Madagascar. Like many other tropical environments worldwide, forests in Madagascar are cut, burnt down, or face other human disturbances. Madagascar has unique ecosystems with species that can only be found on this island, but many of them are threatened with extinction due to forest loss. Some lemur species distribute seeds of the fruits they consume, which helps the forest to grow. Therefore, it is important for them to also use disturbed areas and help the forest to rehabilitate. To determine if three important seed dispersers (red-bellied lemurs, red-fronted lemurs, and common brown lemurs) use degraded areas and those in the process of being restored, my collaborators and I installed camera traps in two forests and nearby restoration areas, as well as in a forest that has recently been burnt. We did not detect the three species in the restoration areas, but the results suggested that the red-bellied lemur and the red-fronted lemur may occur in these areas, but we simply did not detect them with the cameras. The common brown lemurs that we detected in the burnt area appeared to adjust the times of day they were active to cope with the changes in the environment. These results are important to show that these three important seed dispersing species have potential to use disturbed areas and are able to cope with changes in their habitat. If these and other seed dispersing lemurs use disturbed areas, it will also be beneficial for the plant and animal species inhabiting these areas, and our ability to restore them.

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# Appendix 1

**Table S1** Variables and combinations of variables used as detection covariates in the arboreal occupancy models to test which models explain the data best (AIC) for each species. These detection covariates were then used in the arboreal occupancy models including *habitat\_type* (and *deployment\_nr* for *E. rubriventer* and *E. rufifrons*) as occupancy covariate, but only the model with the lowest AIC after including the occupancy covariate was used in the analysis.

Detection covariates with constant occupancy covariates	<i>E. rubriventer</i>	<i>E. rufifrons</i>	<i>E. fulvus</i>
cam_direction	261.8614	127.9762	177.4523
branch_len	226.9336	118.0520	183.7372
branch_diameter	228.6499	118.5349	177.4929
cam_direction + branch_len	231.5353	NA	NA
cam_direction + branch_diameter	234.8619	NA	NA

**Table S2** Variables and combinations of variables used as detection covariates in the terrestrial occupancy model to test which models explain the data best (AIC) for *E. fulvus*. These detection covariates were then used in the terrestrial occupancy model of including *habitat\_type* as occupancy covariate, but only the model with the lowest AIC after including the occupancy covariate was used in the analysis.

Detection covariates with constant occupancy covariates	<i>E. fulvus</i>
cam_direction	188.0001
ground_composition	180.4164
visibility	189.0967
cam_direction + ground_composition	180.6755
cam_direction + visibility	188.9460
ground_composition + visibility	176.2072
cam_direction + ground_composition + visibility	181.3535

**Table S3** Occupancy model output of the arboreal model for *E. rubriventer* showing occupancy and detection estimates for all covariates, and the AIC of the model.

---

*E. rubriventer*

---

Call:  
occu(formula = ~ branch\_len ~ habitat\_type + deployment\_nr, data = UFO1)

---

Occupancy:

	Estimate	SE	z	P(> z )
(Intercept)	0.0771	2.07	0.0372	0.970
habitat_typerestoration	-1.5150	1.34	-1.1311	0.258
deployment_nr	-0.3370	1.22	-0.2758	0.783

---

Detection:

	Estimate	SE	z	P(> z )
(Intercept)	-3.997	1.205	-3.32	0.00091
branch_len	0.206	0.159	1.30	0.19424

---

AIC: 109.7261

---

**Table S4** Occupancy model output of the arboreal model for *E. rufifrons* showing occupancy and detection estimates for all covariates, and the AIC of the model.

---

*E. rufifrons*

---

Call:  
occu(formula = ~ branch\_diameter ~ habitat\_type + deployment\_nr, data = UFO1)

---

Occupancy:

	Estimate	SE	z	P(> z )
(Intercept)	-1.188	1.276	-0.931	0.352
habitat_typerestoration	-1.191	0.987	-1.206	0.228
deployment_nr	0.266	0.879	0.303	0.762

---

Detection:

	Estimate	SE	z	P(> z )
(Intercept)	-2.8896	1.1247	-2.57	0.0102
branch_diameter	0.0736	0.0673	1.09	0.2748

---

AIC: 189.129

---



**Table S5** Occupancy model output of the arboreal model for *E. fulvus* showing occupancy and detection estimates for all covariates, and the AIC of the model.

---

*E. fulvus* arboreal

---

Call:  
occu(formula = ~ branch\_diameter ~ habitat\_type + deployment\_nr, data = UFO1)

---

Occupancy:

	Estimate	SE	z	P(> z )
(Intercept)	5.33	21.3	0.250	0.803
habitat_typeforest	-3.67	21.2	-0.174	0.862
habitat_typerestoration	-12.56	49.4	-0.254	0.799

---

Detection:

	Estimate	SE	z	P(> z )
(Intercept)	-3.240	0.666	-4.86	1.15e-06
branch_len	0.402	0.139	2.89	3.89e-03

---

AIC: 228.5609

---

**Table S6** Occupancy model output of the terrestrial model for *E. fulvus* showing occupancy and detection estimates for all covariates, and the AIC of the model.

---

*E. fulvus* terrestrial

---

Call:  
occu(formula = ~ ground\_composition + visibility ~ habitat\_type + deployment\_nr, data = UFO1)

---

Occupancy:

	Estimate	SE	z	P(> z )
(Intercept)	9.23	51.8	0.17819	0.859
habitat_typeforest	3.65	734.1	0.00497	0.996
habitat_typerestoration	-22.64	358.4	-0.06317	0.950

---

Detection:

	Estimate	SE	z	P(> z )
(Intercept)	-3.61	0.764	-4.72	2.30e-06
ground_composition	-1.25	1.221	-1.02	3.06e-01
visibility	1.00	0.415	2.42	1.55e-02

---

AIC: 173.0833

---

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