BRILL

Folia Primatologica 0 (2023) 1-17

Folia Primatologica

brill.com/ijfp

Updated lemur species ranges in Madagascar's Corridor Forestier d'Ambositra Vondrozo (COFAV)

Carly H. Batist[a,b,*], Michael Bliss[c], David R. Weisenbeck[d], Rija Rafamantanantsoa[e], Georges Razafindrakoto[f], Jerison W. Ranaivosolo[f], Velo Jean Baptiste[f], Patricia C. Wright[g] and Mariah E. Donohue[d]

[a]Department of Anthropology, City University of New York (CUNY) Graduate Center, New York, NY 10016, USA
[b]Rainforest Connection, Katy, TX 77494-6890, USA
[c]Department of Anthropology, Kent State University, Kent, OH 44242, USA
[d]Department of Biology, University of Kentucky, Lexington, KY 40506, USA
[e]University of Antananarivo, Antananarivo, Madagascar
[f]Centre ValBio Research Station, Ranomafana, Madagascar
[g]Department of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364, USA
* Corresponding author; e-mail: cbatist@gradcenter.cuny.edu
ORCID iDs: Batist: 0000-0001-7320-2576; Weisenbeck: 0000-0002-1778-5380; Donohue: 0000-0002-4311-453X

Received 14 February 2023; accepted 3 May 2023; published online 5 June 2023

Abstract – Madagascar's high rates of endemism, paired with its escalating deforestation rates, has made it one of the most important conservation priorities on the planet. In southeastern Madagascar, the Corridor Forestier d'Ambositra Vondrozo (COFAV) is an unprotected rainforest corridor that sustains ~15 species of lemurs, most of which are endangered. The COFAV connects many protected areas and is therefore essential for gene flow, dispersal, and the long-term sustainability of animal populations in the area. The corridor has not been surveyed extensively since the 1990s, and even so, only a fraction of the sites have been sampled multiple times. The goal of our study was to survey the COFAV, from Ranomafana National Park to the Mananara River, to provide updated species occurrences and ranges. Combining data across multiple teams using different inventorying methods, we surveyed a total area of 227 km^2 throughout an eight-month period. We recorded every lemur occurrence (sighting or vocalization) and noted the species, date, time, group size, and GPS coordinates. We found 11 lemur species and one putative hybrid species. The geographic ranges for three species (*Hapalemur aureus*, *H. griseus*, *Propithecus edwardsi*) were larger than previously thought. The range of *Varecia variegata* should be shortened and adjusted accordingly, as the species appears transient (at best) in the northern parts of Ranomafana National Park and was not found south of the Ambohimahamasina/Ikongo region. This study provides updated geographic ranges for lemur species in the COFAV, important information for future censuses, species assessments, and conservation measures for future implementation.

Keywords – *Eulemur*, *Hapalemur*, *Propithecus*, rapid survey, species distribution, *Varecia*.

Introduction

As deforestation and climate change rapidly and devastatingly alter primate habitats worldwide, maintaining up-to-date occurrence data is critical. Filling gaps in primate occurrence data is important because it allows us to better understand the status of primate populations and their habitats, which in turn helps us to develop and prioritize effective conservation strategies. Whilst simplistic, rapid survey assessments and inventories provide valuable data that can inform updated species distributions and occurrences. This is particularly

Published with license by Koninklijke Brill NV | DOI: 10.1163/14219980-bja10012
 | ISSN: 0015-5713 (print) 1421-9980 (online)

important in Madagascar, where high rates of endemism and an escalating deforestation rate have made it one of the most important biodiversity conservation priority areas (Myers *et al*., 2000; Mittermeier *et al*., 2010; Schwitzer *et al*., 2014). Madagascar's enigmatic lemurs are now the most endangered mammals in the world (90% of the 120 species are threatened; Mittermeier *et al*., 2010; Rakotomanana *et al*., 2016; Herrera, 2017). Comprehensive biodiversity surveys are therefore critical for lemur conservation, especially outside of protected areas, within the fragmented forests where many populations of these endangered lemurs live (Irwin *et al*., 2005; Mittermeier *et al*., 2010; Schwitzer *et al*., 2014). These surveys provide crucial information used to update species' range maps, determine their conservation statuses (e.g., via the IUCN Red List), and assess the viability of different populations across fragments and sites (Irwin *et al*., 2005; Rabearivony *et al*., 2015).

The Corridor Forestier d'Ambositra Vondrozo (COFAV) is a humid-forest corridor in southeastern Madagascar that is home to ∼15 species of endangered lemurs (Goodman *et al*., 2001; Irwin *et al*., 2005; Delmore *et al*., 2009). The COFAV is approximately 300 km long, stretching from Ambositra in the north to Vondrozo in the south. It is a relatively narrow tract, ranging from 2-50 km in width, although the majority of the COFAV between Ranomafana National Park (RNP) & Andringitra National Park (ANP) is ∼10 km wide (200-1900 m elevation; Conservation International, 2016; Goodman *et al*., 2001). Previous surveys have recorded this part of the corridor to be between 15-20 km wide, demonstrating that the corridor is continuing to diminish (Goodman *et al*., 2001). Deforestation is being driven by illegal mining, illicit logging, and *tavy* (slash-and-burn agriculture), all of which are increasing at alarming rates (Goodman *et al*., 2001; Irwin *et al*., 2005; Deppe *et al*., 2007; Conservation International, 2016). Hunting/poaching is also a grave concern for lemur species, as many lemurs are hunted for bushmeat or trapped to be sold into the illegal pet trade (Goodman *et al*., 2001; Deppe *et al*., 2007; Borgerson *et al*., 2022). Forest fragmentation in the COFAV is escalating; the remaining continuous forest tract is limited to the high-elevation peaks, as the lowland areas are/have been converted into cropland (Goodman *et al*., 2001; Deppe *et al*., 2007; Ramiadantsoa *et al*., 2015).

The COFAV connects with the Fandriana-Marolambo corridor to the north, part of a network of corridors that provide vital linkage among many national parks and reserves along the eastern region (Irwin *et al*., 2000). These corridors are considered essential for gene flow, dispersal/animal movement, and the long-term sustainability of animal populations in the area (Goodman *et al*., 2001; Irwin *et al*., 2005; Ramiadantsoa *et al*., 2015). Furthermore, the corridor contains an important *Eulemur* hybrid zone; these brown lemur hybrids, which may constitute a separate species, dominate an area around and within ANP, out-competing their parent species (*Eulemur rufifrons* from the north, *E. cinereiceps* from the the south; Johnson and Overdorff, 1999; Johnson, 2002). In the southern part of the COFAV, rivers (i.e., the Manampatrana river, Mananara river) have been suggested to play an important role in both the aforementioned hybrid zone and other lemur species' range limits (Goodman and Ganzhorn, 2004; Irwin *et al*., 2005).

Monitoring efforts in the corridor have been sporadic (see table 1 for summary), so the distribution of the different lemur species is unclear (Sterling and Ramaroson, 1996; Rasoloarison and Rasolonandrasana, 1999; Goodman *et al*., 2001; Irwin *et al*., 2005; Delmore *et al*., 2009). Furthermore, almost all of the previous surveys in the corridor were conducted during the 1990s, so we do not have up-to-date information on lemur ranges within the COFAV (Sterling and Ramaroson, 1996; Rasoloarison and Rasolonandrasana, 1999; Goodman *et al*., 2001; Irwin *et al*., 2005). ANP (eastern slopes) and RNP, historically, have shown similar species assemblages; species described in both parks during early studies include *Propithecus edwardsi*, *Prolemur simus*, *Hapalemur griseus*, *H. aureus*, *E. rubriventer*, *E. rufifrons*, *Microcebus rufus*, *Varecia variegata* and *Daubentonia madagascariensis* (table 1; Goodman *et al*., 2001). However, *V. variegata*

Table 1. Lemur sightings from previous studies in the COFAV, Madagascar.

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Delmore *et al.*, 2009	Ambato Rakanana		x		x	x	x		x						
Delmore *et al.*, 2009	Andavav' Androngo		x	x		x	x		x	x					
Delmore *et al.*, 2009	Ambondro		x	x			x		x						
Delmore *et al.*, 2009	Iharagara		x	x	x		x		x						
Delmore *et al.*, 2009	Ampasy	x	x		x	x	x		x						
Delmore *et al.*, 2009	Ankorabe	x	x		x			x							
Delmore *et al.*, 2009	Ambohitsara	x	x												
Delmore *et al.*, 2009	Ranomena Masakafatsy	x	x												
Delmore *et al.*, 2013[a]	Korokoto				x										
Delmore *et al.*, 2013[a]	Ambarongy				x										
Delmore *et al.*, 2013[a]	Betao				x										
Deppe *et al.*, 2007	Mandriandry		x	x					x	x	x			x	
Gaidet, 1996[b]	Angodongodona									x					
Goodman and Rasolonandrasana, 2001	Andringitra (1,960 m)														

Table 1. (Continued.)

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Goodman and Rasolonandrasana, 2001	Andringitra (1,990 m)		x				x				x	x	x		
Goodman and Rasolonandrasana, 2001	Andringitra (1,625 m)		x			x	x	x			x	x	x	x	x
Goodman and Rasolonandrasana, 2001	Andringitra (1,210 m)		x	x		x	x	x			x	x	x	x	x
Goodman and Rasolonandrasana, 2001	Andringitra (810 m)		x	x		x	x	x	x		x	x			x
Goodman and Rasolonandrasana, 2001	Andringitra (720 m)		x	x		x	x	x	x	?	x	x	x	x	x
Goodman and Rasolonandrasana, 2001	Andringitra (2,050 m)														
Goodman and Rasolonandrasana, 2001	Andringitra (2,450 m)														

Table 1. (Continued.)

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Goodman and Rasolonandrasana, 2001	Andringitra I	x	x	x		x	x	x	x		x	x	x	x	x
Goodman and Rasolonandrasana, 2001	Andringitra II	x	x	x		x	x	x			x	x	x	x	x
Goodman *et al.*, 2001	Andrambovato		x	x			x		x	x	x	x		x	x
Goodman *et al.*, 2001	Mandriandry		x	x		?	x		x	x					x
Goodman *et al.*, 2001	Ambahaka		x	x			x		x	x					x
Goodman *et al.*, 2001	Vinanitelo		x	x			x		x	x	x	x		x	x
Goodman *et al.*, 2001	Ambatambe		x	x		?	x		x	x					
Goodman *et al.*, 2001	Ankopakopaka			x			x		x	x					
Goodman *et al.*, 2001	Manombolo I (1,300 m)		x	x			x		x		x	x		x	x
Goodman *et al.*, 2001	Manombolo II (1,600 m)		x	x		x	x	x	x		x	x			x
Herrera, 2016	Ampatsona		x	x			x		x		x	x	x	x	x
Herrera, 2016	Miaranony		x	x			x		x		x	x	x	x	x
Herrera, 2016	Vohiparara		x	x			x		x		x	x	x	x	x
Herrera, 2016	Maharira		x				x				x	x	x	x	x
Irwin *et al.*, 2000	Marofotsy		x	x			x		x		x		x	x	

Table 1. (Continued.)

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Irwin *et al.*, 2000	Namahoaka		x	x			x		x		x			x	
Irwin *et al.*, 2005	Andringitra		x		x	x	x	x	x						
Irwin *et al.*, 2005	Ivohibe		x	x			x								
Johnson and Overdorff, 1999[a]	Vevembe	x													
Johnson and Overdorff, 1999[a]	Lambohazo	x													
Johnson, 2002	Vevembe	x					x				x	x	x	x	x
Nicoll and Langrand, 1989	Andringitra									x					
Rajaonson *et al.*, 2010	Ambendrana		x			x	x				x				
Rajaonson *et al.*, 2010	Amindrabe					x	x	x	x						x
Rajaonson *et al.*, 2010	Ambodiara					x	x			x					
Rajaonson *et al.*, 2010	Antarehimamy					x	x			x					
Rajaonson *et al.*, 2010	Antaranjaha			x		x	x			x					
Rajaonson *et al.*, 2010	Manambolo		x	x		x									

Table 1. (Continued.)

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Rakotondravony *et al.*, 2004[c]	Andrambovato					x									
Rakotondravony *et al.*, 2004[c]	Vinanitelo					x									
Rakotondravony *et al.*, 2004[c]	Manambolo I					x									
Rakotondravony *et al.*, 2004[c]	Manambolo II					x									
Rakotonirina *et al.*, 2013	Fandana					x	x								
Rakotonirina *et al.*, 2013	Ambalavero					x	x			x					
Rakotonirina *et al.*, 2013	Vohitrambo									x					
Rasoloarison and Rasolonandrasana, 1999	Corridor (1,200 m)		x	x							x	x		x	
Rasoloarison and Rasolonandrasana, 1999	Corridor (900 m)		x	x			x				x	x		x	

Table 1. (Continued.)

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Rasoloarison and Rasolonandrasana, 1999	Ivohibe (1,200 m)			x			x				x	x		x	
Rasoloarison and Rasolonandrasana, 1999	Ivohibe (1,575 m)		x	x			x				x	x			
Rasoloarison and Rasolonandrasana, 1999	Ivohibe (900 m)		x	x			x				x	x	x	x	
Sterling and Ramaroson, 1996	Andringitra (1,625 m)		x			x	x	x			x	x	x	x	x
Sterling and Ramaroson, 1996	Andringitra (1,210,m)	x	x	x		x	x				x	x	x	x	
Sterling and Ramaroson, 1996	Andringitra (810 m)	x	x			x	x	x	x		x	x			x

Table 1. (Continued.)

Reference	Site	*E. cinereiceps*	*E. rubriventer*	*E. rufifrons*	*Eulemur* hybrids	*H. aureus*	*H. griseus*	*P. simus*	*P. edwardsi*	*V. variegata*	*M. rufus*	*Cheirogaleus* sp.	*Lepilemur* sp.	*Avahi* sp.	*D. madagascariensis*
Sterling and Ramaroson, 1996	Andringitra (720 m)	x	x						x		x	x	x	x	x
Wright *et al.*, 2008[d]	Miaranony							x							
Wright *et al.*, 2008[d]	Ambatolahy							x							
Wright *et al.*, 2008[d]	Talatakely							x							
Wright *et al.*, 2008[d]	Manambolo							x							
Wright *et al.*, 2008[d]	Korokoto							x							
Wright *et al.*, 2012[d]	Ranomafana		x	x		x	x	x	x	x	x	x	x	x	x

[a]Only surveyed for *Eulemur* hybrids.
[b]Only surveyed for *V. variegate*.
[c]Only surveyed for *H. aureus*.
[d]Only surveyed for *P. simus*.

has not been found in or around ANP during more recent surveys, suggesting they may now be locally extinct in this area (table 1; Irwin *et al*., 2005; Delmore *et al*., 2009). *Varecia* are considered an effective indicator species for forest health, as they rarely live in degraded forest due to their reliance on large fruiting trees (Balko, 1998). Further, only one *P. simus* individual remains in RNP and the species has only been sporadically documented in the rest of the COFAV, seemingly due to low density and fragmented populations (table 1; Wright *et al*., 2008). Species within nocturnal genera such as *Cheirogaleus*, *Avahi* and *Lepilemur* are also found in both parks, but there has been debate over whether these represent the same species or different ones (e.g., *L. mustelinus* vs. *L. microdon*, *C. major* vs. *C. crossleyi* vs. *C. grovesi*, *A. laniger* vs. *A. peyrierasi*; Sterling and Ramaroson, 1996; Rasoloarison and Rasolonandrasana, 1999; Goodman *et al*., 2001; Wright *et al*., 2012).

Studying lemur populations in regions of the COFAV that have not been sampled in decades is essential for updating species ranges and better understanding their conservation status. Our goal for this study was to survey a portion of the COFAV, from the northern limit of Ranomafana National Park to the Mananara River, to provide updated occurrence data and ranges for lemur species in the region. The corridors between ANP and Ivohibe as well as ANP and Vondrozo/Vevembe have been sampled even less than the corridor between ANP and RNP, so our results from the latter area will be particularly important for establishing southern range limits of lemur species. We conducted rapid survey assessments, which have proven effective in determining lemur presence and species richness (Sterling and Ramaroson, 1996; Deppe *et al*., 2007; Delmore *et al*., 2009). We combined data from multiple teams to get as complete of a picture as possible of lemur occurrences in the COFAV. While this heterogeneous data collection approach does introduce caveats and limits the analyses possible, our goal was to maximize the quantity of inventory data we had. By comparing our results to those of previous studies, we can evaluate how lemur ranges may have changed in the COFAV over the past few decades.

Methods

Opportunistic sampling teams (OPP1 and OPP2)

OPP1 surveyed 27 sites from the north of Ranomafana National Park up to Andringitra National Park from December 2021-May 2022 (fig. 1, supplementary table S1). OPP2 surveyed 14 sites spaced approximately 15-20 km apart from Sandranata (near Fianarantsoa) to Vevembe (near Vondrozo) from January-August 2022 (fig. 1, supplementary table S1). Our lemur sighting data was collected opportunistically while doing fieldwork for larger projects. OPP1 was focused on using passive acoustic monitoring to record lemur calls (to be analyzed using machine learning detection models). OPP2 was focused on collecting fecal samples for a *Eulemur* population genomics study across the hybrid zone and peripheral parental species ranges (*E. rufifrons* to the north and *E. cinereiceps* to the south).

OPP teams recorded every time lemurs were seen or heard while hiking through the forest. For each of these events, we noted: day and time, lemur species, a GPS point (Garmin eTrex 20), group size (if possible) and group composition (age and sex classes, if possible). We also noted anecdotal information we received from local villagers at some sites about lemur species' presence in the area. Both teams visited each site twice.

Transect team (TRN)

TRN traveled to two areas within the COFAV to conduct transect-based surveys. The two areas were Ankarimbelo (Beizi and Sahahita) and Bemahala (fig. 1, supplementary table S1). TRN conducted transects at Ankarimbleo in May and Bemahala in June. TRN surveyed two locations within the Ankarimbelo region. The first location at Beizi was ∼1 km outside of the forest periphery and the second location at Sahahita was ∼4 km outside the forest boundary towards the interior (fig 1). TRN established

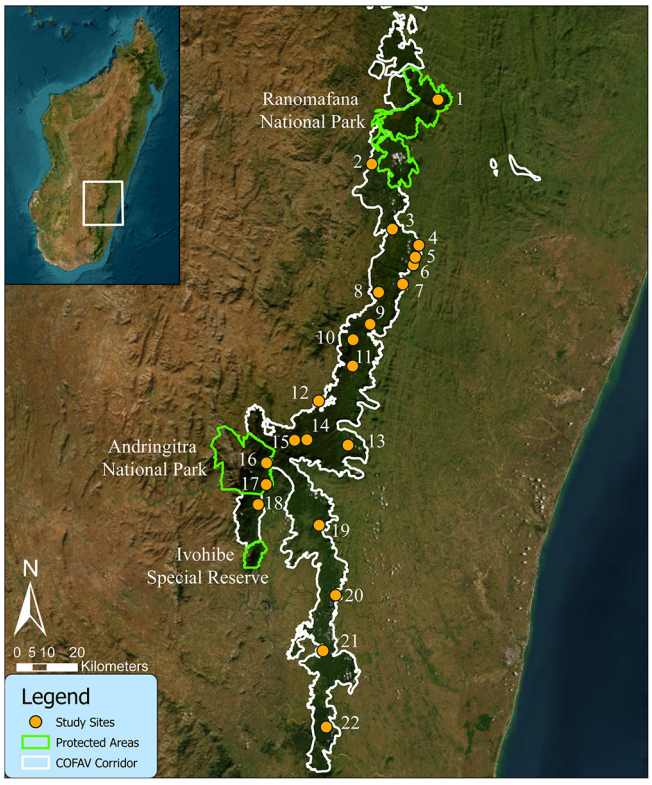

Figure 1. Map of the COFAV corridor (white outline) and connected protected areas (green outline). In the inset map (top left corner), the white box outlines the total study area. Numbered points indicate the location of each study site. 1) Namahoaka; 2) Maharira; 3) Ambalavero; 4) Mandriandry; 5) Malazamasina; 6) Antanivelona; 7) Sahafoza; 8) Andranomiditra; 9) Vinanitelo Sud; 10) Sandranata; 11) Itoalana/Lovasoa; 12) Lomaka; 13) Ankarimbelo; 14) Vohembe; 15) Ankona; 16) Ambarongy; 17) Ampasy; 18) Marandrano; 19) Emma; 20) Manasara; 21) Vevembe; 22) Bemahala. Basemap data from UNEP-WCMC & IUCN (2023) and Esri *et al.* (2023).

the transects' placements, directions and team starting points randomly.

TRN conducted surveys for a total of one week at each location. They established four 1-km transects at each location and marked every 50 m from start to finish. Two subsets (two people) of TRN surveyed the transects at ~1 km/hour. For each lemur occurrence (seen or heard) we recorded the following information: date and time, lemur species, a GPS coordinate (Garmin etrex10), elevation, distance of the lemurs from the transect at 90 degrees, group size and group composition (age-class and sex). Each team performed two transects on four continuous days (32 total diurnal surveys), alternating the starting position (start or end points) to randomize surveys. Alternating starting positions enabled TRN subsets to arrive at the 50 m points along the transects at various times to account for diel variation. Both TRN subsets also surveyed two transects on alternating nights (16 total nocturnal surveys). TRN surveyed one location within the Bemahala region. The original goal for this area was to replicate the sampling design from Ankarimbelo, but this was not possible due to security concerns. However, they were able to perform surveys at one location ~1.5 km inside the forest periphery for two days and one night. TRN established two 1-km transects and conducted 8 total diurnal surveys and 4 total nocturnal surveys using the same methods outlined for Ankarimbelo.

Prior to surveying at each site, TRN also conducted informal interviews with community forest management groups (VOIs, Vondron'Olona Ifotony), to determine which lemur species were present before and after the 2022 cyclones (Batsirai and Emnati). TRN asked the forest officials to describe the physical appearances of lemurs without showing illustrations and verified these descriptions using field guides (Mittermeier *et al*., 2010). The Ankarimbelo VOIs are especially prudent, conducting biweekly patrols throughout the forest to monitor for illegal activities and record lemur sightings. The Bemahala VOI only monitors the forest semi-annually due to security concerns.

Data analysis

Data points were mapped using ArcGIS Pro (v.3.1.1) onto a global imagery basemap (Esri *et al*., 2023). With these data, we sought to (1) describe each species distribution throughout the COFAV and (2) identify their southernmost extent. We also calculated demographic summary statistics for each species, including average group size and presence/absence of juveniles and infants. Finally, we compared the number of diurnal lemur species observed at each site to identify sites with high species richness. However, we did not test for significant differences in demography or species richness because field methods and effort (i.e., number of searching hours) varied considerably across sites and teams.

Results

In total, we encountered lemurs 172 times from December 2021 to August 2022 (fig. 2, supplementary table S1). We encountered 11 species and one putative hybrid species: *Avahi* spp. (25 detections, two sites), *Cheirogaleus* spp. (two detections, two sites), *D. madagascariensis* (one detection, one site), *E. rubriventer* (23 detections, eight sites), *H. aureus* (12 detections, seven sites), *H. griseus* (11 detections, six sites), *Microcebus* spp., (one detection, one site), *P. edwardsi* (13 detections, seven sites), *V. variegata* (36 detections, 10 sites). We note that only TRN team conducted nocturnal surveys; nocturnal lemur sightings by the OPP teams were near campsites at dusk. As such, fig. 1 contains observations from all taxa identified to the species level. We also encountered brown lemurs (*E. cinereiceps*, *E. rufifrons*, hybrids) throughout the COFAV, but cannot delimit hybrid zone boundaries without genomic data (in prep.). Amalgamated across the species complex, brown lemurs were spotted 48 times at 16 sites.

All diurnal species were detected at multiple sites in the COFAV between Ranomafana and Andringitra (fig. 2, supplementary table S1,). *V. variegata* had the shortest distribution, with no encounters south of the Lovasoa VOI (southernmost sighting). Our southernmost *P. edwardsi* sighting was Andrinigtra. Brown lemurs, *E. rubriventer*, *H. aureus*, and *H. griseus* were all detected south of Andringitra. *H. aureus* was not detected south of Emma. *E. rubriventer* was not detected south of Manasara. *H. griseus* was not detected south of Vevembe. Brown lemurs had the longest distribution and were detected at every site, including Bemahala.

Rapid demographic assessments across species showed variation in group size and make-up (supplementary table S1). On average, *E. rubriventer* groups had 2.73 $\pm$ 0.98 (standard deviation) individuals, with a range of one to five. *H. aureus* and *H. griseus* had average group sizes of 3 $\pm$ 1.87 (range: 1-5) and 1.8 $\pm$ 0.79 (range: 1-2), respectively. The average *P. edwardsi* group size was 3.5 $\pm$ 0.85 (range: 2-5). The average *V. variegata* group size was 1.5 $\pm$ 0.58 (range: 1-2). Finally, across all three species of brown lemur, the average group size was 5.9 $\pm$ 3.55 (range: 1-18). Brown lemurs were the only species observed with infants. Infants were spotted from March to April in two sites, Lomaka and Lovasoa. Juveniles were observed in groups of brown lemurs, *E. rubriventer*, and *H. aureus*.

Diurnal lemur species richness varied across sites. The site with the highest observed lemur diversity was Sandranata, with eight species total. Seven species were observed in Ankarimbelo and Itoalana/Lovasoa, four species were observed in Lomaka and Emma, three lemur

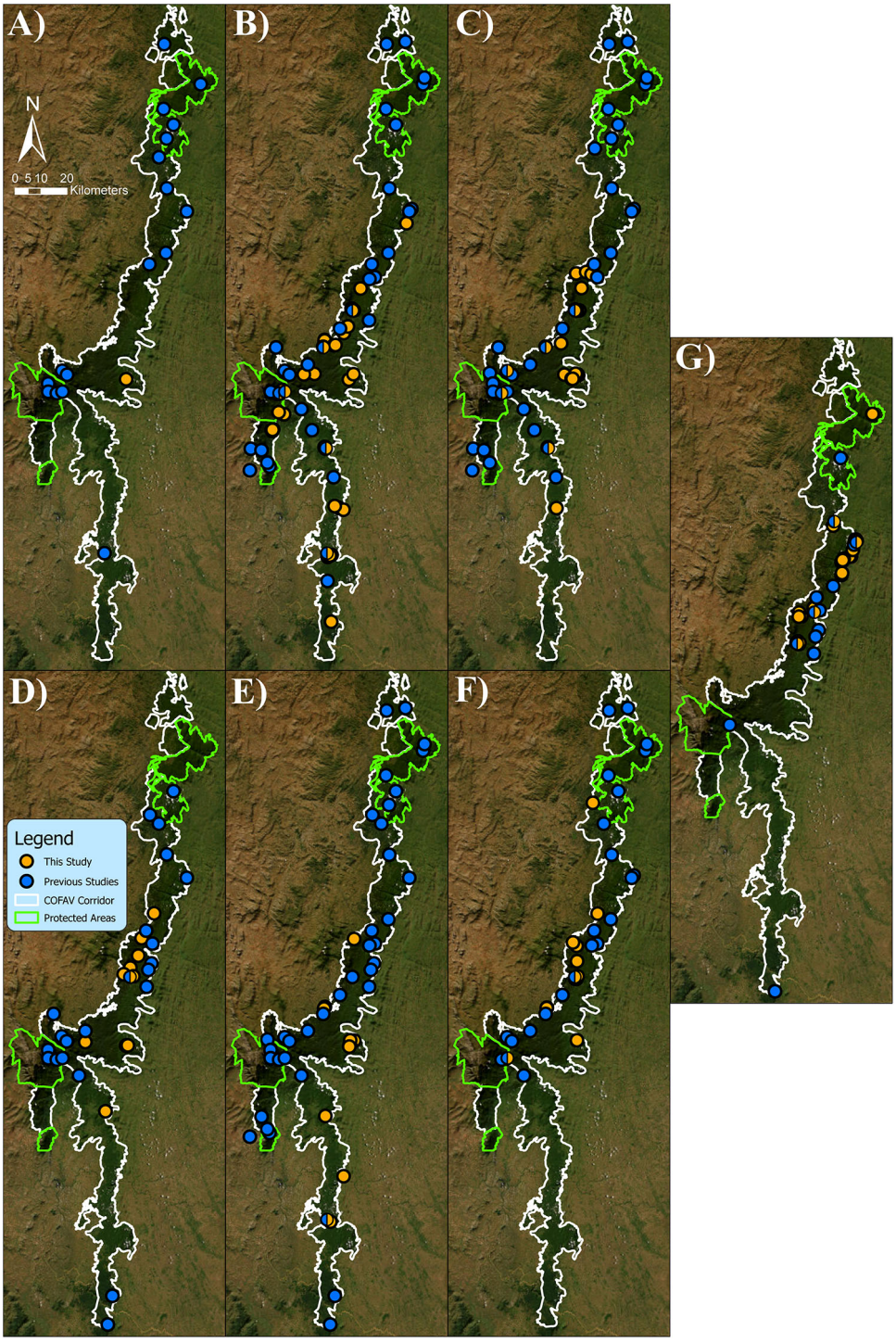

Figure 2. Map of lemur records from previous studies (blue) and this study (orange) for each species encountered in this study. A) *Daubentonia madagascariensis*; B) Brown lemurs; C) *Eulemur rubriventer*; D) *Hapalemur aureus*; E) *H. griseus*; F) *Propithecus edwardsi*; G) *Varecia variegata*. Basemap data from UNEP-WCMC & IUCN (2023) and Esri *et al*. (2023).

species were observed in Ambarongy, Manasara and Vinanitelo Sud. Only two species were observed in Andranomiditra, Antanivelona, Vevembe, and Vohembe and just one species was detected in Ambalavero, Ampasy, Ankona, Bemahala, Maharira, Malazamasina, Mandriandry, Marandrano, Namahoaka, and Sahafoza.

TRN's interviews with local naturalists revealed possible effects of Cyclone Batsirai on lemur distribution in Ankarimbelo. Two species, *P. simus* and *V. variegata*, were present before the cyclone but had not been seen since. Locals in Bemahala reported no change in species presence/absence after the cyclone.

Discussion

To our knowledge, this study is the first to survey Madagascar's COFAV corridor in the new millennium. We sought to revise known and predicted lemur species distributions from Ranomafana National Park to the Mananara River (∼227 km). We took advantage of transect surveys, opportunistic sightings, and informal interviews with local communities to infer as comprehensive an understanding as possible of lemur occurrence in the COFAV. We confirmed the presence of 11 lemur species throughout this region. We discovered four taxa – an unknown *Cheirogaleus* species, *H. aureus*, *H. griseus*, and *P. edwardsi* – further south than is currently listed on IUCN RedList (Irwin *et al*., 2020; Wright *et al*., 2020a, b). We did not detect *V. variegata* south of the Ambohimahamasina and Ikongo region, suggesting a recent contraction in the range of this Critically Endangered species. Further, we only heard one individual north of RN25 (the highway bisecting Ranomafana National Park) and VOI members reported only rarely hearing lone individuals; the species therefore appears to be only transient in this region. This study is one of the most comprehensive surveys of the COFAV, as most previous studies only focused on a few sites (Sterling and Ramaroson, 1996; Rasoloarison and Rasolonandrasana, 1999; Goodman *et al*., 2001; Irwin *et al*., 2005; Delmore *et al*., 2009). The most extensive survey beforehand was conducted in the 1980s-1990 s (Goodman *et al*., 2001; Irwin *et al*., 2005). Given the considerable changes in land-use, human population size and forest cover during the past 30 years, our study provides a much-needed update of lemur ranges throughout the COFAV.

These findings highlight the need for conservation action and research in under-studied, unprotected, yet incredibly biodiverse regions of the COFAV. The high species richness found at some sites underscores the importance of forest corridors as refuges for fragmented lemur populations (Rabearivony *et al*., 2015; Ramiadantsoa *et al*., 2015; Herrera, 2017); the same almost certainly holds true for other endangered Malagasy species as well (e.g., fossa, tenrecs, *Mantella* frogs, etc.). The importance of the COFAV in connecting existing national parks and sustaining lemur populations throughout the region warrants the inclusion of corridors into Madagascar's protected area system (Delmore *et al*., 2009; Herrera, 2017; Coldrey and Turpie, 2021). While some sites in the COFAV are home to many lemur species, many sites visited during this study were highly degraded. We ourselves witnessed extensive *tavy* (slash-and-burn agriculture), mining, logging, and areas of deforestation within the corridor. Deforestation in this region, as in many parts of Madagascar, is largely driven by the need to convert land into rice paddies and livestock grazing fields (Goodman *et al*., 2001; Irwin *et al*., 2005; Conservation International, 2016). Without formal protection at multiple administrative levels, the COFAV is at severe risk of disappearing in the very near future. This would isolate lemur populations into protected parks and refugia, limiting dispersal and genetic variation.

With climate change and global warming increasing, cyclones in the Indian Ocean basin are becoming stronger, more frequent, and making landfall in Madagascar further south than ever before (Weiskopf *et al*., 2021). Just during the span of this study, two of the strongest cyclones to ever hit Madagascar (Batsirai and Emnati) made landfall along the coast that parallels the COFAV. The cyclones caused widespread destruction within communities and forests, with extensive tree-falls, landslides, and floods. As cyclones increase in frequency and

strength, the COFAV will be at risk of further deforestation, fragmentation and decreased food availability for animals.

The methods used to complete these rapid assessments of COFAV lemur biodiversity varied across time, space, and field teams. OPP1 and OPP2 teams were not systematically searching for lemurs; rather, they were recording sightings and vocalizations opportunistically. Conversely, TRN conducted deliberate searches for lemurs, devising transects to optimize sightings and accurately depict the sampling population. Additionally, while TRN explicitly conducted nocturnal surveys, OPP1 and OPP2 did not, creating a significant bias favoring the detection of diurnal species at all but the two field sites visited by TRN. Further, OPP1 and OPP2 conducted research throughout the entire eight-month project duration, whereas TRN team only surveyed during the peak of the cold/dry season (June-July), when many nocturnal species undergo hibernation or torpor. Nevertheless, data collected using different methods can still be useful for certain use cases, such as inventories. While it is ideal to start from the beginning of a collaboration and use standardized methods, this may not be feasible if primatologists are looking to use existing datasets. By combining datasets, such as we have done in this study, more comprehensive sampling is possible.

Although this collaborative study contains some preliminary limitations, systematic surveys are essential for monitoring lemur (and all primate) populations over time and space. In the future, conducting standardized transect-based surveys (similar to the methods used by TRN team) during day and night will be critical for comprehensively sampling diurnal and nocturnal lemur assemblages. Furthermore, surveys should be conducted throughout the year to account for seasonal variations within and across species. Finally, combining these survey data with site-specific environmental information (e.g., phenology, floristic species richness) would allow researchers to better understand the ecological factors affecting lemur population dynamics in the COFAV. These preliminary surveys will hopefully serve as a catalyst for further research in the COFAV. This corridor, despite increasingly high rates of deforestation, still harbors a rich assemblage of endemic species and should be prioritized for future conservation efforts and initiatives.

Acknowledgement

All authors are grateful to the VOIs we worked with, for welcoming and supporting us. The Conservation International team in Fianarantsoa, Forêt office in Ambalavao and Centre ValBio research station staff all provided vital logistical support. For support and advice, CHB thanks Dr. Andrea Baden, MD thanks Dr. David Weisrock, and MB thanks Laura Verbeek. CHB also thanks Solo and Honoré for maintaining camps and keeping our team well-fed. MB thanks Velo and all of our local guides for their hard work, hospitality, and impeccable lemur spotting/tracking abilities. MB also thanks Noel for maintaining our campsites and for his great, much-needed conversations by the fire after long field days. CHB was funded by the Fulbright US Student program, Primate Conservation Inc (#1673), American Society of Mammalogists, CUNY Graduate Center Provost's Digital Innovations Grant, CUNY Graduate Center Doctoral Student Research Grant, and the CUNY Graduate Center Early Research Initiative. MB was funded by a grant from Re:Wild (#SMA-CCO-G0000000045). MD was funded by the Fulbright US student program, Primate Conservation Inc (RWPF #52), University of Kentucky Ribble Pilot Grant, University of Kentucky Morgan Fellowship, University of Kentucky Dean's Competitive Fellowship.

Author contributions

CHB, MB and MD conceived and designed the study with support from PCW. CHB, MB, RR, GR, VJB, WR and MD carried out data collection. MD conducted data analysis. CHB, MB and MD drafted the manuscript. CHB, MD and DRW carried out revisions. All authors approved the final version.

Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.23176484

References

Balko EA (1998). *A behaviorally plastic response to forest composition and logging disturbance by Varecia variegata variegata in Ranomafana National Park, Madagascar*. PhD dissertation. State University of New York College of Environmental Science and Forestry.

Borgerson C, Johnson SE, Hall E, Brown KA, Narváez-Torres PR, Rasolofoniaina BJR, Razafindrapaoly BN, Merson SD, Thompson KET, Holmes SM, Louis EE, Golden CD (2022). A national-level assessment of lemur hunting pressure in Madagascar. *International Journal of Primatology* 43(1): 92–113.

Coldrey KM, Turpie JK (2021). The future representativeness of Madagascar's protected area network in the face of climate change. *African Journal of Ecology* 59(1): 253–263.

Conservation International (2016). Environmental and social management plan. In *Sustainable Landscapes in Eastern Madagascar*, pp. 1–135.

Delmore KE, Brenneman RA, Lei R, Bailey CA, Brelsford A, Louis Jr EE, Johnson SE (2013). Clinal variation in a brown lemur (*Eulemur* spp.) hybrid zone: combining morphological, genetic and climatic data to examine stability. *Journal of Evolutionary Biology* 26(8): 1677–1690.

Delmore KE, Keller MF, Louis Jr EE, Johnson SE (2009). Rapid primatological surveys of the Andringitra forest corridors: direct observation of the greater bamboo lemur (*Prolemur simus*). *Lemur News* 14: 49–52.

Deppe AM, Randriamiarisoa M, Schütte K, Wright PC (2007). A brief lemur survey of the Ranomafana Andringitra corridor region in Tolongoina, southeast Madagascar. *Lemur News* 12(12): 43–46.

Esri, Maxar, Earthstar Geographics, GIS User Community (2023). World imagery [basemap]. ESRI. https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9. Accessed 15 March 2023.

Gaidet N (1996). *Inventaire des Oiseaux et des Lémuriens d'un Couloir Forestier du Massif D'Andringitra. Rapport Non-Publié*. Madagascar, World Wildlife Fund.

Goodman SM, Ganzhorn JU (2004). Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *Journal of Biogeography* 31(1): 47–55.

Goodman SM, Rasolonandrasana BP (2001). Elevational zonation of birds, insectivores, rodents and primates on the slopes of the Andringitra Massif, Madagascar. *Journal of Natural History* 35(2): 285–305.

Goodman SM, Razafindratsita V, Schütz H, Ratsimbazafy R (2001). Les Lémuriens. In *Inventaire Biologique du Parc National de Ranomafana et du Couloir Forestier qui la Relie au Parc National D'Andringitra* (Goodman S, Razafindratsita V, eds.), pp. 231–243. Antananarivo, Madagascar, Recherches pour le Développement, Série Sciences Biologiques.

Herrera JP (2016). Interactions between plants and primates shape community diversity in a rainforest in Madagascar. *Journal of Animal Ecology* 85(4): 982–993.

Herrera JP (2017). Prioritizing protected areas in Madagascar for lemur diversity using a multidimensional perspective. *Biological Conservation* 207: 1–8.

Irwin M, Frasier CL, Louis EE (2020). *Hapalemur griseus*. The IUCN Red List of Threatened Species 2020: e.T9673A115564580. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T9673A115564580.en. Accessed on 2 January 2023.

Irwin MT, Johnson SE, Wright PC (2005). The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx* 39(2): 204–218.

Irwin MT, Smith TM, Wright PC (2000). Census of three eastern rainforest sites north of Ranomafana National Park: preliminary results and implications for lemur conservation. *Lemur News* 5: 20–22.

Johnson SE (2002). *Ecology and speciation in brown lemurs: white-collared lemurs* (*Eulemur albocollaris*) *and hybrids* (*Eulemur albocollaris* × *Eulemur fulvus rufus*) *in southeastern Madagascar*. PhD dissertation. The University of Texas at Austin.

Johnson SE, Overdorff DJ (1999). Census of brown lemurs (*Eulemur fulvus* sspp.) in southeastern Madagascar: methods-testing and conservation implications. *American Journal of Primatology* 47(1): 51–60.

Mittermeier RA, Louis EEJ, Richardson MJ, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J,

Rasoloarison R, Roos C, Kappeler PM, MacKinnon J (2010). *Lemurs of Madagascar (Tropical Field Guide Series)*, 3rd ed. Arlington, VA, Conservation International.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000). Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853–858.

Nicoll ME, Langrand O (1989). *Madagascar: Revue de la conservation et des aires protégées*. WWF-Fonds Mondial Pour la Nature.

Rabearivony J, Rasamoelina M, Raveloson J, Rakotomanana HV, Raselimanana AP, Raminosoa NR, Zaonarivelo JR (2015). Roles of a forest corridor between Marojejy, Anjanaharibe-Sud and Tsaratanana protected areas, northern Madagascar, in maintaining endemic and threatened Malagasy taxa. *Madagascar Conservation & Development* 10(2): 85–92.

Rajaonson A, Ratolojanahary M, Ratsimbazafy J, Feistner A, King T (2010). Enquête préliminaire de la distribution des lémuriens de bambou dans et autour du Corridor forestier Fandriana-Vondrozo, Madagascar. *Lemur News* 15: 34–39.

Rakotomanana H, Jenkins RK, Ratsimbazafy J (2013). Conservation challenges for Madagascar in the next decade. In *Conservation Biology: Voices From the Tropics* (Raven N, Sodhi S, Gibson L, eds.), pp. 33–390. Hoboken, NJ, Wiley-Blackwell.

Rakotondravony D, Razafindramahatra LV (2004). Contribution à l'étude des populations de *Hapalemur aureus* dans le couloir forestier Ranomafana-Andringitra. *Lemur News* 9: 28–32.

Rakotonirina LHF, Rajaonson A, Ratolojanahary JH, Missirli JM, Fara LR (2013). Southern range extensions for the critically endangered black-and-white ruffed lemur *Varecia variegata* and greater bamboo lemur *Prolemur simus*. *Primate Conservation* 26(1): 49–55.

Ramiadantsoa T, Ovaskainen O, Rybicki J, Hanski I (2015). Large-scale habitat corridors for biodiversity conservation: a forest corridor in Madagascar. *PLOS One* 10(7): e0132126.

Rasoloarison R, Rasolonandrasana BPN (1999). Les lémuriens. In *Inventaire Biologique de la Réserve Spéciale du pic D'Ivohibe et du Couloir Forestier qui la Relie au Parc National D'Andringitra* (Goodman SM, Rasolonandrasana BPN, eds.), pp. 159–169. Antananarivo, Madagascar, Recherches pour le Développement, Série Sciences Biologiques.

Schwitzer C, Mittermeier RA, Johnson SE, Donati G, Irwin M, Peacock H, Ratsimbazafy J, Razafindramanana J, Louis EE, Chikhi L, Colquhoun IC, Tinsman J, Dolch R, Lafleur M, Nash S, Patel E, Randrianambinina B, Rasolofoharivelo T, Wright PC (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science* 343(6173): 842–843.

Sterling EJ, Ramaroson MG (1996). Rapid assessment of the primate fauna of the eastern slopes of the Reserve Naturelle Integrale d'Andringitra, Madagascar. In *A Floral and Faunal Inventory of the Eastern Slopes of the Réserve Naturelle Intégrale D'Andringitra, Madagascar: with Reference to Elevational Variation* (Goodman S, ed.), pp. 293–305. Fieldiana, Zoology.

UNEP-WCMC and IUCN (2023). Protected Planet: The World Database on Protected Areas (WDPA) [GIS dataset]. Cambridge, UK: UNEP-WCMC and IUCN. https://www.protectedplanet.net. Accessed 15 March 2023.

Weiskopf S, Cushing J, Morelli TL, Myers B (2021). Climate change risks and adaptation options for Madagascar. *Ecology and Society* 26(4).

Wright PC, Erhart EM, Tecot S, Baden AL, Arrigo-Nelson SJ, Herrera J, Morelli TL, Blanco MB, Deppe A, Atsalis S, Johnson S, Ratelolahy F, Tan C, Zohdy S (2012). Long-term lemur research at Centre ValBio, Ranomafana National Park, Madagascar. In *Long-Term Field Studies of Primates* (Kappeler PM, Watts DP, eds.), pp. 67–100. Berlin, Heidelberg, Springer.

Wright PC, Johnson SE, Irwin MT, Jacobs R, Schlichting P, Lehman S, Louis EE, Arrigo-Nelson SJ, Raharison JL, Rafalirarison RR, Razafindratsita V, Ratsimbazafy J, Ratelolahy FJ, Dolch R, Tan C (2008). The crisis of the critically endangered greater bamboo lemur (*Prolemur simus*). *Primate Conservation* 23(1): 5–17.

Wright PC, Hearthstone E, Andrianoely D, Donohue ME, Otero-Jiménez BJ (2020a). *Propithecus edwardsi*. The IUCN Red List of Threatened Species 2020: e.T18359A115573104. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T18359A115573104.en. Accessed on 02 January 2023.

Wright PC, Hearthstone E, Donohue ME, Andrianoely D, Otero-Jiménez BJ, Lauterbur ME (2020b). *Hapalemur aureus*. The IUCN Red List of Threatened Species 2020: e.T9672A115564398. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T9672A115564398.en. Accessed on 02 January 2023.