Going, Going, Gone...Is the Iconic Ring-tailed Lemur (*Lemur catta*) Headed for Imminent Extirpation?[†]

Lisa Gould¹ and Michelle L. Sauther²

¹Department of Anthropology, University of Victoria, Victoria, BC, Canada ²Department of Anthropology, University of Colorado, Boulder, CO, USA

Abstract: The ring-tailed lemur (*Lemur catta*) was once widely distributed throughout the south-central, far south, and southwest regions of Madagascar. This species is known for its marked ecological plasticity and ability to survive in a variety of habitats. Over the past decade, however, habitat destruction, forest fragmentation, hunting for subsistence or the illegal bushmeat trade, and live capture for the illegal pet trade have increased, resulting in extirpation or drastic reduction of populations throughout its geographic range. Recent mining activities in one region have resulted in further serious threats to remaining populations. In this paper, we discuss (1) population numbers and information on population extirpations, gathered over approximately the past six years, to illustrate the alarming decline of this well-known lemur, and (2) how the formerly accepted geographic range of *L. catta* now requires considerable revision. Population information was collected via on-the-ground surveys and censuses, or from reports by researchers at 34 sites where *L. catta* is or was recently present. Only three sites are known to contain populations of more than 200 animals. At 12 sites, populations number 30 or fewer individuals, and at 15 sites, *L. catta* has been recently extirpated, or populations are highly precarious and may become extinct in the very near future. Populations at three previously designated range limits have been extirpated. Many populations are surviving in small, isolated forest fragments, allowing for no male dispersal. With an estimate of just 2,000–2,400 individuals remaining in Madagascar, this iconic lemur may well become extinct in the wild in the near future, or at the very least, exist at only two or three widely dispersed sites.

Key Words: Lemur catta, local extinction, forest fragments, population decline, hunting, pet trade

Introduction

Populations of the iconic ring-tailed lemur (*Lemur catta*) were once widespread throughout varied habitats in southern, southwest and south-central Madagascar, largely due to this species' considerable ecological plasticity (Sauther *et al.* 1999; Sussman *et al.* 2003, 2006; Goodman 2006; Gould 2006; Gould and Gabriel 2015; Gould *et al.* 2015; Sauther *et al.* 2015). *Lemur catta* inhabits at least seven distinct habitats (Goodman *et al.* 2006; Gould 2006; Cameron and Gould 2013), and is able to adapt to local environmental extremes and natural disasters, for example, arid open spiny bush, with temperatures reaching or exceeding 45°C and

with little available water (Sauther et al. 1999; Gould et al. 2011; Kelley 2011; LaFleur 2012), severe droughts (Gould et al. 1999), and cyclones (LaFleur and Gould 2009). However, anthropogenic habitat loss in the geographic range of L. catta is steadily increasing (Sussman et al. 2003; Harper et al. 2007; La Fleur 2013), and in 2003, Sussman et al. noted that remaining populations were unevenly distributed with very low densities. Since then, loss of forest cover throughout southern Madagascar has only increased, largely due to anthropogenic deforestation (Sussman et al. 2006; Bodin et al. 2006; Harper et al. 2007; Kelley et al. 2007; ONE et al. 2013a, 2013b), with little regeneration due to the xerophytic nature of much of the flora in the region (Seddon et al. 2000; Fenn 2003). Average rates of annual forest loss in protected areas (national parks and special reserves) in L. catta's geographic range were reported as 0.28% per year from 2000-2005, and 0.22% per year from 2005-2010 (ONE et al. 2013a, 2013b); however, these data do not take

[†] This paper is dedicated to the memory of Robert W. Sussman (1941–2016), highly respected scholar and pioneer of lemur studies.

into account the considerable amount of unprotected area in which *L. catta* has been reported. Furthermore, an increase in serious droughts in the south over the past decade has also exacerbated habitat loss (Elmqvist *et al.* 2007; Tengo and von Heland 2014). Sussman *et al.* (2006) estimated that *L. catta* habitat loss totaled 10% between 1985 and 2000, with a 20% reduction in the total population.

In 2001, Sussman et al. (2003) conducted a broad survey of L. catta in the south-western and far southern portions of its geographic range. At that time, forest fragmentation was noted as a marked threat to L. catta population survival. Since then, further and significant forest loss and increased fragmentation throughout southern Madagascar has been documented (Bodin et al. 2006; Harper et al. 2007; Cameron and Gould 2013). Fortunately, due to their ecological flexibility, ring-tailed lemurs in some regions are able to live, and in some cases, even thrive, in small fragments, particularly "sacred forests"-small patches containing Malagasy ancestral graves and tombs. Such forests range in size from <1 to 142 ha in the far southern Androy region (Tengo et al. 2007; Kelley 2011) and 2 to 53 ha in the south central area of L. catta's geographic range (Gould and Andrianomena 2015; see Table 1). Sacred forests are normally undisturbed and can contain sufficient food and water resources to allow L. catta population persistence, reproduction and survival (Bodin et al. 2006; Gould and Gabriel 2014; Gould and Andrianomena 2015). However, the increasing fragmentation throughout southern Madagascar in the past decade, as well as heavy hunting for the illegal bushmeat trade and capture for the illegal pet trade, have resulted in the extirpation or drastic reduction of ring-tailed lemur populations at many sites where they are or were found (Sussman et al. 2006; Kelley et al. 2007; Cameron and Gould 2013; Sauther et al. 2015; Gould and Andrianomena 2015; LaFleur et al. 2015; Actman 2016; Reuter et al. 2016). As a result, the IUCN Red List status for L. catta was upgraded from Near Threatened to Endangered in 2012 (Andriaholinirina et al. 2014).

Historically, the geographic range of Lemur catta was broad, covering the southwestern, south-central, and southern portion of the island (Hill 1953; Tattersall 1982; Goodman et al. 2006). Its wide-ranging dispersal is due to its ability to survive and reproduce in areas that can be considered ecologically marginal, such as spiny bush and spiny thicket, high altitude ericoid bush, small rocky outcrop fragments, and mangroves (Goodman et al. 2006; Gould et al. 2006; Sauther et al. 2013). Ring-tailed lemurs are not restricted by river systems, and can survive in areas without a ground water source (Goodman et al. 2006). Goodman et al. (2006) also noted that since many river systems in southern Madagascar are without water for some months during the dry season, and since L. catta have been noted at gallery forest sites to cross these dry riverbeds, such ranging ability may have promoted wide geographic dispersal. However, continual anthropogenic habitat disturbance, habitat loss, and population extirpations have resulted in a much smaller geographic range than that outlined by Goodman et al. in 2006.

In this paper, we present *L. catta* population numbers and densities, or presence/absence information, mostly gathered over the past six years, covering 34 sites throughout this species' geographic range: south-central Madagascar, the far south, and the southwest. These sites include protected areas such as national parks, special reserves, and private reserves, as well as unprotected areas. We note the decline, and, in some cases, extirpation or likely extirpation, of the *L. catta* populations inhabiting some of these sites, and we also suggest a revision of the former boundaries of the geographic distribution of the ring-tailed lemur.

Methods

Population information was collected either via census counts by research teams, or census/survey and presence/ absence reports in the literature, covering 34 sites where *L. catta* is or was recently present (Fig. 1). For the majority of sites, information was obtained within the past six years (Table 1).

South-central Madagascar

Censuses were conducted by Lisa Gould and team in 2013 in nine small (between 2 and 53 ha) forest fragments in south-central Madagascar, as part of a larger study of ecological factors driving population persistence or extinction (Gould and Cowen, in prep.; Fig. 2). The sites are situated in a 370-km² mountainous area and are, according to local guides with whom Gould worked, the only forest fragments containing *L. catta* in the region, outside of Andringitra National Park. Seven of the nine sites are protected by community-level

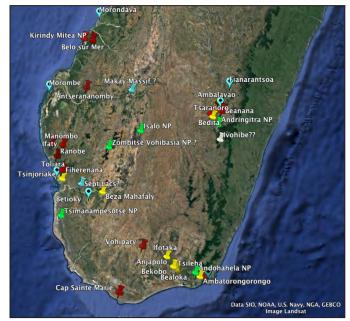


Figure 1. Known sites in the geographic range of *Lemur catta* where populations are extant, likely extirpated, or recently extinct. Red pins = extirpated or near extirpated populations, yellow pins = extant populations, green pins = national parks, where some populations are extant, others unknown and may be extinct, and blue pins = unknown, reported locally within the past 15 years but not seen during surveys.

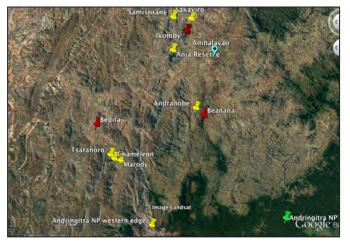


Figure 2. Sites in the south-central region of Madagascar where *Lemur catta* was surveyed and censused in 2013 by L. Gould and team.



Figure 3. Sites in the far southern region where *Lemur catta* was surveyed and censused in 2015 by Foulon *et al.* (2015).

conservation associations (Gould and Andrianomena 2015). Two of these, Anja Private Reserve and Tsaranoro Valley forest, are well-known tourist destinations. The two unprotected fragments have been seriously affected by firewood collection and forest degradation.

Census collection teams were composed of LG, as well as primary guide P. Andrianomena, and assistants J. Weir, and S. Rasoanomenjanahary. We were assisted by local guides from the above mentioned community-based conservation groups at the seven community-run sites. At each site, the census team counted all resident adult and juvenile (yearling) lemurs. Juveniles are easily determined as they are roughly half the size of adults. Animals were counted by each team member at least twice, and all counts fell within a two-animal margin of error. In smaller fragments (20 ha or fewer in size, see Table 1) all *L. catta* groups were located and members were counted over a period of one to three days. At the larger Anja and Tsaranoro forests, censuses took place over four to five days.

Andringitra and Isalo national parks are situated in southcentral Madagascar. Gould and team counted two *L. catta* groups in Andringitra National Park in 2009. *Lemur catta* is also found at Isalo (Goodman *et al.*, 2006; LaFleur, pers. comm. 2016; Madagascar, MNP 2015).

Southern Madagascar

In Madagascar's far south, census data were collected on L. catta residing in nine forest fragments by Foulon et al. (2015). These fragments included the larger and well-known Berenty Reserve, 80 km from Taolagnaro (Fort-Dauphin), as well as a number of much smaller gallery forest fragments along the Mandrare River (Fig. 3). All lemurs were counted by the census team at least twice. The numbers of extant L. catta groups at Ifotaka-North (approximately 50 km north of Berenty), and Vohipary, a remote spiny forest fragment 55 km NW of Ifotaka, were noted in 2012, but individuals were not counted (Sterman 2012; Semel and Ferguson 2013). At Ambatotsirongorongo (approximately 25 km west of Taolagnaro), L. catta was censused by Razafindramanana in 2009, and at Petriky, the southeasternmost site in which L. catta has been recorded (Goodman 2006), individuals were counted by Malone et al. (2013) in 2012 (Fig. 4). Cap Sainte-Marie is the southernmost point at which L. catta has been recorded (Goodman et al. 2006). Animals were counted by Kelley (2011) during a year-long dissertation study in 2007–2008. The last census of L. catta at Andohahela National Park was conducted in 2003 (Rasoarimanana 2005).

Southwestern Madagascar

Individual animals have been counted at Bezà Mahafaly Reserve (Sauther and Cuozzo 2008; Sauther, 2014) and Tsinjoriake (Ravelohasindrazana 2013; Ravoavy 2013; I. A. J. Youssouf, pers. comm. 2016). Presence/absence of *L. catta* only was noted at Ifaty (I. A. J. Youssouf, pers. comm. 2016), as well as at Fiheranana-Manombo and Ranobe (Gardner *et al.* 2009), Makay forest (Dolch *et al.* 2012; Wendenbaum *et al.* 2014) and Antsirananomby (Kelley *et al.* 2007). Historically, *L. catta* were recorded at three national parks in the southwest: Kirindy-Mitea, Tsimanampesotse, and Zombitse-Vohipary. Presence/absence, but not population counts have been reported at Kirindy-Mitea (R. J. Lewis, pers. comm. 2015) and Zombitse-Vohipary (M. Sauther, pers. obs.) and a partial population count is available for Tsimanampesotse (Sauther *et al.* 2014; M. LaFleur pers. comm.) (Fig. 5).

Area measurements of 17 fragments were calculated (1) using the polygon tool in Google Earth, and (2) polygon location points were entered into the Earthpoint tools KML Shapes program (<<u>http://www.earthpoint.us/Shapes.aspx</u>>) to determine actual fragment size in hectares. Areas of other sites were gathered from the literature.

Results

Table 1 lists all the sites discussed here, geographic locations, *L. catta* population counts or presence/absence estimates, population densities where possible, and forest sizes in hectares. At eight sites (Petriky, Ranobe, Kirindy-Mitea National Park, Antsirananomby, Vohipary, Makay,

Gould and Sauther

Table 1. Site names, locations, population counts or estimates, forest sizes, and population densities (where applicable) for the 34 known sites where *Lemur catta* are or were recently extant. Total population estimates are listed at the bottom of each larger region: south-central, southern, and southwestern Madagascar. n/d = no data.

Site and Location Total N = 34 sites	Year of count or estimate and number of <i>L. catta</i> counted or estimated	Forest size and population density (where applicable)
outh-central Madagascar (N=12)		
Anja Community Reserve South-central 21°51'S, 46°50'E	2013: c. 210 (Gould and Andrianomena 2015)	34 ha (6.2/ha)
Sakaviro Community Reserve 21°48>S, 46°52'E	2013: c. 30 (Gould and Andrianomena 2015)	7.7 ha (3.8/ha)
amisorany 1°47'S, 46°49'E	2013: 21 (Gould and Andrianomena 2015)	20.3 ha (1.03/ha)
Indranobe 1°57'S, 46°55'E	2013: 30 (Gould and Andrianomena 2015)	17.4 (1.7/ha)
leanana 1°57'S, 46°56'E	2013: <i>c</i> . 6 (Gould and team, census) Likely extirpated in 2016	20.7 ha (0.28/ha)
saranoro Valley forest 2°05'S, 46°46'E	2013: 78 (Gould and Andrianomena 2015)	53 ha (1.47/ha)
hameleon 2°05'S, 46°46'E	2013: 28 (Gould and Andrianomena 2015)	8.1 ha (3.4/ha)
1arody 2°05'S, 46°47'E	2013: 15 (Gould and Andrianomena 2015) Precarious	2.8 ha (5.3/ha)
komby 1°48'S, 46°51'E	2013: 8 (L. Gould and team, census) Likely extirpated in 2016	2 ha (4/ha)
Bedita 2°02'S, 46°43'E	2013: c. 15–20 (L. Gould and team, census) Precarious	Forest fragment not measured
ndringitra National Park (Western edge) 2°12' S, 46°53'E	2009: Estimate <i>c</i> . 100 (WWF guide, 2009) but likely fewer: 12 counted in 2009 (L. Gould, D. N. Gabriel and A. Cameron)	31,160 km ²
salo National Park 2°22'S, 45°11'E	Extant but number unknown	81,500 ha
Estimate of L. catta at known sites the south-central egion	c. 600–700 individuals	
outhern Madagascar (N=13)		
Berenty Reserve (all parcels and environs, including gal- ery, scrub, spiny forests + tourist and factory areas) 5°34'S,46°18'E	2015: 562 (Foulon et al. 2015)	285 ha (2.0/ha)
Bealoka 4°57'S,46°16'E	2015: 163 (Foulon et al. 2016)	100 ha (1.63/ha)
sileha 4°57'S,46°14'E	2015: 39 (Foulon et al. 2016)	48 ha (0.81/ha)
ekobo 4°56'S, 46°13'E	2015: 21 (Foulon et al. 2016)	52 ha (0.40/ha)
nalalava 4°56'S, 46°12'E	2015: 21 (Foulon et al. 2016)	95 ha (0.22/ha)
njapolo 4°55'S, 46°13'E	2015: 70 (Foulon <i>et al.</i> 2016)	104 ha (0.67/ha)
mbinany 4°59'S, 46°18'E	2015: 65 (Foulon et al. 2016)	60 ha (1.08/ha)
mbatorongorongo 5°04'S, 46°46'E	2010: <i>c</i> . 50 in 30ha (Razafindramanana 2011)	30 ha (1.5/ha)
etriky 5°03'S, 46°52'E	2012: 4 animals in 920 ha. Likely extirpated (M. Malone, pers. comm.)	920 ha (0.004/ha)
ohipary 4°36'S, 45°33'E	2012: 1 small group (individuals not counted) (Sterman 2012) Precarious or possibly extirpated in 2016	1250 ha
fotaka-North-Protected Area 4°45'S, 26°04'E	2012: 3 groups (individuals not counted) (B. P. Semel, pers. comm.) Precarious	22, 256 ha (Mahamaro 2012)
'ap Sante-Marie 5°27'S, 45°06'E	2007: 4-5 groups in 2007 (Kelley 2011, 2013) Status in 2016 unknown	<i>c</i> . 0.017/ha (Kelley 2013)

table continued on next page

Site and Location Total N = 34 sites	Year of count or estimate and number of <i>L. catta</i> counted or estimated	Forest size and population density (where applicable)
Andohahela National Park 24°59'S, 46°40'E	2003: 118 (Rasoarimanana 2005) Status unknown 2016, hunting reported (Raharivololona and Ranaivosoa 2000; Madagascar Biodiversity Fund, undated)	76,000 ha
Estimate of <i>L. catta</i> at known sites in the far southern region	c. 1000 individuals	
Southwestern Madagascar (N = 9)		
Beza Mahafaly Reserve All parcels 23°41'S, 44°22'E	2014: <i>c</i> . 200 (Sauther 2014)	Parcel 1: 80 ha (124 animals - 1.5/ha) All parcels: 900 ha
Tsinjoriake 23°26'S, 43°45'E	2016: 27 (I. A. J. Youssouf, pers. comm.) Precarious	25,000 ha (0.01/ha)
Fiheranana-Manombo complex and Ranobe 23°14'S, 43°52'E 22°48'S, 43°44'E	2009: (3) data deficient Likely extirpated (Gardner <i>et al.</i> 2009)	n/d
Ifaty forest 22°48'S, 43°28'E	2016: Precarious or possibly extirpated Hunting and live capture threat (I. A. J. Youssouf, pers. comm.)	n/d
Antsirananomby 21°42S, 44°8′E	2004: observed 10 times, 5 were of a lone individual (Kelley <i>et al.</i> , 2007) Status unknown likely extirpated 2016	Forest fragmented and degraded
Makay Massif 21°41'S, 45°04'E	2012: 2 surveys, none observed Possibly extirpated Dolch <i>et al.</i> (2012), Wendenbaum <i>et al.</i> (2014)	n/d
Kirindy Mitea National Park Southwest 20°03'S, 44°39'E	2012: 2 seen at Ankoatsifaka in 2012, none since. Likely extir- pated in 2016 (R. J. Lewis, pers. comm. 2015).	152,000 ha (0/ha)
Tsimanampesotse National Park 24°03'S, 43°46'E	2006-2014: <i>c</i> . 80–100. 11 groups counted between 2006–2014 (Sauther <i>et al.</i> 2013; M. LaFleur, pers. comm.) Live capture threat (La Fleur <i>et al.</i> 2015)	456 km ² (0.18/ha)
Zombitse-Vohibasia National Park 22°45'S, 44°37'E	Status unknown Likely extirpated (M. Sauther, pers. obs.)	36,308 ha (density likely 0/ha)
Estimate of <i>L. catta</i> at known sites in the southwestern region	c. 350 individuals	
Total population estimate based on populations at known sites	<i>c</i> . 2000–2400 individuals	



Figure 4. Sites at the far southeastern limit of the range of *Lemur catta*. Note that at Petriky, formerly the southeastern-most site where *L. catta* was found (Goodman *et al.* 2006), the population is likely now extirpated.

Fiheranana-Manombo, and Zombitse-Vohibasia National Park), ring-tailed lemurs were reported present until recently, but population sizes were very low (for example, at Petriky, only four lemurs were present in 2011, Table 1). Some of these populations are now likely extirpated. At five sites (Bedita, Beanana, Ifotaka North, Ifaty, and Tsinjoriake) populations



Figure 5. Sites in the southwestern region of the range of *Lemur catta* where populations are extant or recently extinct.



Figure 6. The former geographic distribution of *Lemur catta* (based on Goodman *et al.* 2006).

are low and threatened by forest disturbance and/or heavy hunting pressure/live capture for the illegal pet trade. These are listed as "Precarious" or "Likely extirpated" in Table 1.

The former geographic distribution, proposed by Goodman *et al.* in 2006, is no longer accurate, due to recent population extirpations. Sites that were considered the northwestern (Kirindy-Mitea National Park and Belo sur Mer), northeastern (Ankafina), and southeastern (Petriky) limits of the range of *L. catta* (Goodman *et al.* 2006) no longer contain populations of ring-tailed lemurs. At Cap Sainte-Marie, the southernmost point of the geographic range of *L. catta*, four to five groups were present in 2007 (Kelley 2011), but no surveys have been conducted at this site since then.

Figures 6 and 7 reflect the old and newly proposed distributions. Population estimates of *L. catta* for each region are as follows: south-central Madagascar *c.* 600–700; southern Madagascar: *c.* 1000; and southwestern Madagascar: *c.* 350. The estimated total population of *L. catta* at known sites in the wild is *c.* 2000–2400 (Table 1).

Discussion

While this is not an exhaustive survey or census of every site inhabited by *Lemur catta*, the information in Table 1 represents all *known* populations and population extirpations as of 2016. Recent local extinctions, the known number of very small populations (*c*. 30 individuals or fewer) inhabiting small and isolated forest fragments, lack of continuous forest throughout the known range of *L. catta*, and the shrinking geographic range limits (Fig. 7) demonstrate that this well-known lemur is in rapid and alarming decline. In 2012, the IUCN Red List status of *L. catta* was upgraded from Near Threatened to Endangered, an increase of two categories. This designation was based partially on some of the data included in this paper (Andriaholinirina *et al.* 2014). Considering population



Figure 7. The current geographic distribution of *Lemur catta* based on information contained in this paper.

assessments over the past six years, and current threats to this species, it is clear that more local extinctions are on the horizon, and in August 2016, *L. catta* was placed on the list of the IUCN SSC Primate Specialist Group's "World's 25 Most Endangered Primates" (Schwitzer *et al.* in prep.).

Habitat fragmentation has been noted as a severe threat to this species since 2003 (Sussman et al. 2003). Since then, significant forest loss in most areas of the geographic range of L. *catta* means that more and more populations are now residing in small, isolated habitat remnants. Recent serious increases in illegal hunting for food for the black market bushmeat trade, and live capture for the illegal pet trade (Sauther et al. 2013; LaFleur et al. 2015; Reuter et al. 2016; I. A. J. Youssouf, pers. comm.) have decimated populations; local extinctions have occurred where L. catta was formerly abundant, and many remaining populations persist at extremely low numbers. These populations will likely be extirpated in the near future if they have not been already (for example, Zinner et al. 2001; Kelley et al. 2007; Gardner et al. 2009; Wendenbaum et al. 2013; Lemur Conservation Network 2015; Madagascar Biodiversity Fund, undated).

South-central Madagascar

The south-central plateau region contains no large, continuous tracts of forest, only scarce, small forest fragments dispersed throughout the landscape (Cameron and Gould 2013; Gould and Andrianomena 2015). This area contained far more forest cover just a few decades ago (J. N. Rabialahy, pers. comm.), but deforestation and fragmentation has reduced L. catta populations in this region to very low numbers, living in isolated patches surrounded by agriculture and villages. A survey by L. Gould and team in 2013 revealed only nine fragments within a 370-km² region that contained L. catta populations. The Anja Private Reserve and the Tsaranoro Valley forest are well-protected community operated, tourist destinations, where L. catta populations are the most numerous in the region (Table 1). Anja exhibits the highest population density of L. catta of any forest sampled; however, the 13 groups of lemurs inhabiting the reserve are crowded into a small area of 34 ha, with highly overlapping home ranges. Three smaller forests, Sakaviro, Samisorany, and Andranobe, are also community protected but without the tourism potential of the two larger sites. These smaller fragments contained small but seemingly healthy populations of ring-tailed lemurs in 2013, relative to fragment size, and in all of the above forests, food and water resources were sufficient for population survival (Gould and Cowen, in prep.). Other small fragments in the region were also surveyed. Two of these, Chameleon and Marody, were protected by villagers and each contained a very small population of L. catta, while the others (Ikomby, Bedita, Beanana) were unprotected, with regular tree-cutting and firewood collection. The latter three fragments contained very low numbers of lemurs in 2013, and population extirpation has likely occurred or is imminent. Six of the nine fragments surveyed in this region are too isolated to allow for male dispersal and gene flow, as they are either spaced too

far from one another (for example, 7 to 18 km in the cases of Anja Reserve and Andranobe), or the landscape between fragments consists of roads, a major highway, numerous villages, agriculture, and large tracts of open savannah with no trees to allow for foraging, sleeping, or protection from predators. Such isolation is likely to result in dangerous losses of genetic variation (Davies and Schwitzer 2013; Clarke *et al.* 2015) if these populations survive. The remaining three sites, the Tsaranoro, Chameleon and Marody forests, are situated in the Tsaranoro Valley, and allow for some male dispersal, but the total *L. catta* population of the valley numbered only 121 individuals in 2013, and fires set for cattle grazing very near these small forests often burn out of control.

Both the Isalo and Andringitra national parks in this region have L. catta populations, but their sizes are unknown. Goodman and Langrand (1996) reported a potentially isolated group of eight high-altitude-dwelling L. catta at the upper elevations of the Andringitra Massif, near Pic Ivangomena (2,520 m elevation), but noted that these animals were threatened by frequent fires in the low density ericoid bush that they inhabited. In 2009, Gould and her team located two groups in the same region of the park, and counted 12 animals. Goodman and Langrand (1996) suggested, and we concur, that the number and density of this population is very low, as L. catta here are restricted to a small area of high-altitude ericoid bush at the western edge of the park. During observations in 2009, local people harassed the lemurs, despite the presence of WWF guides and the research team. It is unknown whether this population is still extant.

Lemur catta is also stated as present at Pic d'Ivohibe Special Reserve, 20 km south of Andringitra National Park (Travel Madagascar, undated), but again, no surveys or censuses have been conducted. No trails or tourism infrastructure exist at this site, thus it is unclear if *L. catta* are extant or protected there.

There are ring-tailed lemurs at Isalo National Park (M. LaFleur, pers. comm. 2016), but the total population number is unknown. The park is vast (81,000 ha), and there is at least one small population in one area of the park, which tourists visit and photograph.

Southern Madagascar

Madagascar's far south, stretching from Petriky and Andohahela National Park through Cap Sainte-Marie and inland, is characterized by spiny bush, occasional gallery forest, and a semi-arid climate with little annual rainfall (Bodin *et al.* 2006; Kelley 2011). In 2006, Bodin *et al.* noted that much of the far southern spiny forest ecoregion was severely fragmented and had been so for several decades, if not hundreds of years, but that many of the fragments were protected by local taboos (sacred forests). At the time of the Bodin *et al.* study, however, such traditional taboos were eroding, and the authors predicted a successive loss of forest patches in this area. Ringtailed lemurs were found in a number of these small fragments throughout the far south, and, as seed dispersers, are or were, an essential aspect of the health of these small forests (Bodin *et al.* 2006; Tengo and von Heland 2014).

The best known of the southern sites is Berenty Reserve, a gallery forest managed by the de Heaulme family since 1936 (Jolly et al. 2006). The L. catta population there has remained relatively stable for decades (Jolly et al. 2006). The population of the reserve itself and surrounding environs is the largest currently known, at c. 560 animals (Foulon et al. 2015). Lemur catta populations of varying sizes are also found in six smaller gallery forests north of Berenty, following the course of the Mandrare River (Foulon et al. 2015). These forests are relatively isolated from one another, and separated by sisal plantations and agriculture (Fig. 3), but some male dispersal may be possible. The Ifotaka Community Forest is 24 km north of these fragments, and in 2012 three unprotected groups of L. catta were recorded there (Semel and Ferguson 2013), but were often chased by village dogs (B. P. Semel, pers. comm.). Lemur research at Ifotaka North was halted in 2013 due to the proliferation of small firearms used by, and the increased activity of, cattle thieves (dahalo), who burn villages and displace local people inhabiting the area; people who might otherwise protect the sacred forest patches (B. P. Semel and B. Ferguson, pers. comm.).

In 2007, two ring-tailed lemur groups, totaling only 24 individuals, were followed by Kelley at Cap Sainte-Marie (Kelley 2011), but the population fell to 17 during the year-long study. Both groups ranged outside of the Cap Sainte-Marie Special Reserve, in spiny thicket habitat, and were two of only four to five groups found in the region at that time.

Goodman *et al.* (2006) noted that the most easterly record of *L. catta* was at Petriky, a transitional zone between wet and dry forest, 32 km southwest of Taolagnaro (Fort-Dauphin) (Malone *et al.* 2013). During a survey of this forest, Malone *et al.* observed *L. catta* only twice, and only four lemurs were counted (M. Malone, pers. comm. 2012). The easternmost site where *L. catta* has been counted recently is Ambatorongorongo, 25 km west of Taolagnaro (Fort-Dauphin), where 50 animals were seen in 2009 (Razafindramanana 2011).

An extensive survey and census of *L. catta* was conducted at Andohahela National Park, north of Taolagnaro, between 1999 and 2003 (Raharivololona and Ranaivosoa, 2000; Rasoarimanana 2005). In 2003, only 118 individuals were counted. There have been no more recent surveys in the park, and hunting pressure in the area has been high for some time (Rasoarimanana 2005; Bucht 2011). *Lemur catta* was also reported to inhabit gallery forests west of Kalambatritra Massif in the southeast in the early 2000s, but information was anecdotal, and no ring-tailed lemurs were actually observed (Irwin 2001). Again, no recent surveys have been reported in this area, although a survey and action plan for the Kalambatritra Special Reserve was being planned in 2013 (Rasolofoharivelo *et al.* 2013).

South-western Madagascar

Lemur catta was once widely distributed along the west coast of Madagascar, from the Kirindy-Mitea region near

Morondava, south through Tsimanampesotse National Park and Cap Sainte-Marie in the far south (Tattersall 1982; Sussman et al. 2003). These western forests have become severely fragmented over the past five decades, with a 10% overall loss between 1950 and the 1990s (Zinner et al. 2001), and the landscape has fragmented even further in the 15 years since the Zinner et al. study (Google Earth 2016). Much forest in this region was destroyed for maize production in the 1990s (Zinner et al. 2001; Kelley et al. 2007; Blanc-Pamard 2009), and Sussman et al. (2003) noted that significant deforestation had occurred in the southwest between 1985 and 2000 for grazing, small-scale farming, and charcoal production. Recent additional and significant threats to west-coast forests are the Toliara Sands mining project and oil exploration (Gardner 2009; Blanc-Pamard 2009; Huff 2016; Lemur Conservation Network 2015).

Kirindy-Mitea National Park and Belo-sur Mer were considered the north-western limits of L. catta's distribution (Goodman et al. 2006); however, the population in this area is now considered extirpated—the last observation of L. catta in Kirindy-Mitea occurred in 2012, and consisted of just two individuals (R. J. Lewis, pers. comm. 2015). As far back as 1999, local people in the region outside of the national park reported that L. catta had not been seen in the area for years (Zinner et al. 2001). Similarly, Kelley et al. (2007) noted that the formerly lush forest of Antserananomby, east of Morombe, had, by 2004, been largely destroyed by slash-and-burn agriculture for maize crops. Only a few small fragments remained, and the gallery forest no longer existed. Heavy hunting of the remaining lemurs was apparent. In the 1960s and 1970s, Antserananomby was considered to have the highest primate density and diversity of any forest in western Madagascar (Sussman 1972; Sussman et al. 2006). This is the site where pioneer L. catta researcher Robert Sussman conducted his Ph.D. research in the early 1970s. In the 2004 survey, Kelley et al. observed L. catta only 10 times, and five of these observations were of just one individual. Furthermore, at least four lemur traps were observed during this survey.

Dolch *et al.* (2012) and Wendenbaum *et al.* (2013) found no *L. catta* in the Makay Massif, west of Morondava, even though ring-tailed lemurs had previously been reported there. Wendenbaum *et al.* (2013) suggested that heavy hunting, particularly in temporary hunting/fishing camps, as well as large-scale forest clearing for cattle grazing, will likely have reduced or extirpated any populations in the area.

Recent serious increases in hunting for the illegal bushmeat trade and live capture for the purposes of selling infant *L. catta* to hotels along the coast has severely affected ringtailed lemur populations (Sauther *et al.* 2013; I. A. J. Youssouf, pers. comm.)—some are now extirpated and others persist at extremely low densities and are markedly threatened (Gardner *et al.* 2009; Sauther *et al.* 2013; Lemur Conservation Network, 2015). The Toliara Sands mining project seriously affects the Mikea forest, the Fiherenan-Manombo complex and the Ranobe forest. This project will have major negative impacts on local people and wildlife, including the potential destruction of sacred forests, heightened exposure to radiation from mine tailings, and the destruction of vast areas of forest (Gardner *et al.* 2009; Huff 2016; Environmental Justice Atlas 2015, Lemur Conservation Network 2015). With the addition of hunting pressure, several populations of *L. catta* in this region along the coast have been extirpated and others are now found in extremely low numbers (Gardner *et al.* 2009; Gardner and Davies 2014). Oil exploration is also occurring on the west coast and southwestern inland (Blanc-Pamard 2009; Caravel Energy Limited 2013; Environmental Justice Atlas 2015).

South of Toliara, significant deforestation occurred in 2013 to make way for new hotels (M. Sauther, pers. obs.). The Sept Lacs Region near Toliara along the Onilahy River contained key areas of gallery forest and wetland that in 2003 included numerous vulnerable species, including L. catta, although only presence/absence data are currently available (Emmett et al. 2003). The area was originally slated for ecotourism development and even as a national protected area as part of "The Durban Vision" (Tilghman et al. 2005). In 2004, however, an artisanal sapphire rush around the area of the village of Ifanato, near one of the lakes, brought in miners from other areas who hunted the local wildlife, including lemurs, to feed themselves (Tilghman et al. 2005). A 2014 report stated that while some of the habitat and lakes had been destroyed, WWF and the local community had recently worked to protect the remaining forest (Madonline 2014). Tourist circuits were developed, and local guides were trained to lead visitors through the area. It is currently unknown if or how many lemurs remain at this site.

The recently protected Tsinjoriake site is found between 15 km and 25 km south of Toliara. This site is composed of approximately 25,000 ha of limestone cliffs, southwestern dry spiny bush and coastal mangroves (Sauther *et al.* 2013). Eight ring-tailed lemur groups were reported at two locations during a survey in April, 2012, including groups using the local mangrove forests to obtain fresh water (Ravelohasin-drazana 2013; Ravoavy 2013). In one area surveyed in 2016, however, just 27 individuals were counted (I. A. J. Youssouf, pers. comm. 2016), and the groups no longer used areas of the mangrove forest due to the large number of dogs in the area.

Lemur catta still occurs at the Bezà Mahafaly Reserve, a gallery forest research site inland from Toliara on the Mahafaly Plateau. The reserve, composed of two parcels, was established in the mid-1980s, and the population has remained stable since 1985, with a total of around 200 *L. catta* in both parcels of the reserve (Sauther and Cuozzo 2008; Sussman *et al.* 2012; Sauther 2014; Ranaivonasy *et al.* 2016). Due to 1) the stability of this population, 2) the large relatively intact gallery forest within the reserve, and 3) the degraded but habitable forest fragments around the reserve, the Bezà Mahafaly *L. catta* is an important source population (as per Pulliam 1988). While the population within the reserve has remained relatively constant over the years, a comparison of satellite images from 1990 and 2010 revealed that the unprotected forest surrounding the first reserve parcel had decreased by

20%, the second parcel had experienced some forest loss, and the forest contiguous to the second parcel had decreased by 50% in 20 years (Ranaivonasy *et al.* 2016). It is unknown if *L. catta* populations exist in other forest patches on the Mahafaly Plateau; during the 1990s very small, remnant, and isolated populations were observed in a few places, but the status of these in 2016 is not known. Thus, even there, there is cause for concern.

Ring-tailed lemurs were observed at Zombitse-Vohibasia National Park, north of Bezà Mahafaly Reserve, in 2001, but at a very low density, as they were heavily hunted (Sussman *et al.* 2003). It is unknown whether any remain in the park in 2016. A population of *L. catta* can still be found at the Tsimanampesotse National Park (LaFleur 2012; Sauther *et al.* 2013; LaFleur and Sauther 2015), although the total number of animals is unknown, as the park is large and, in places, inaccessible. Part of the population, containing around 80–100 animals, is continually monitored via long-term studies by M. LaFleur, and by M. Sauther and F. P. Cuozzo (Sauther *et al.* 2013; LaFleur *et al.* 2014; LaFleur and Sauther 2015). There are recent reports, however, of infants being taken for the illegal pet trade (LaFleur *et al.* 2015).

Conclusion

The information in this paper summarizes the population status at the majority of sites where *L. catta* are or have been reported, and demonstrates that this well-known lemur is in very serious and rapid decline, with a total estimation from known sites throughout their geographic range of only

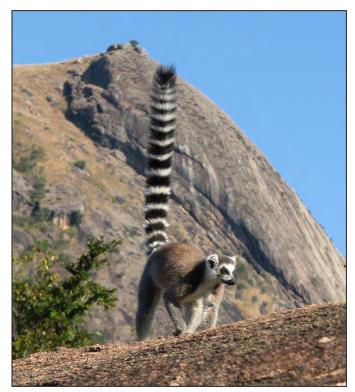


Figure 8. *Lemur catta* at Tsaranoro Valley rocky outcrop forest, south-central Madagascar.

c. 2,000–2,400 animals. In most areas, populations of ringtailed lemurs are shrinking, and numerous local extinctions in the past decade have been caused by deforestation for cattle grazing, agriculture, and charcoal production. Such deforestation has led to severe habitat fragmentation and local extinctions. Fires set in grassland areas to encourage re-growth for cattle grazing can spread to nearby small forest fragments inhabited by *L. catta* and rapidly destroy them. Hunting for the illegal bushmeat trade and live capture for the pet trade has taken its toll on many former populations, and in some regions, traditional taboos against harming ring-tailed lemurs have eroded. Additional pressures include long-term mining and oil exploration concessions.

It would be extremely useful if thorough surveys and censuses could be conducted in the national parks where *L. catta* is still known to exist: Andringitra, Tsimanampesotse, and Isalo. These parks contain large tracts of forest and shelter *L. catta* populations, but much of the terrain in these parks would be highly challenging to traverse. However, technology such as drones outfitted with thermal imaging cameras could be used to enter difficult-to-access areas. Such surveys and censuses could take several months, but it would be most beneficial to know the size of populations in these protected areas. Surveys should also be undertaken at Andohahela National Park, the Cap Sainte-Marie region, and Kalambatritra and Pic d'Ivohibe special reserves to determine if *L. catta* is still present or now extinct.

Only three known sites, relatively small reserves, contain populations of over 200 animals: Berenty Reserve, Bezà Mahafaly Reserve, and Anja Private Reserve, but Anja is a fragment with little to no possibility for male dispersal. Berenty and Bezà Mahafaly reserves do allow for male dispersal and, given the relative stability of these populations, these areas can be seen as potential source populations, which should receive conservation priority, and empirical studies should focus on source-sink dynamics (Furrer and Pasinelli 2016) in such areas.

The outlook for *Lemur catta* seems grim, particularly outside of the handful of truly protected areas in which they live. The ring-tailed lemur is a remarkably ecologically flexible species, capable of surviving and thriving even in harsh habitats and through natural disasters (for example, Sauther *et al.* 1999; Gould *et al.* 1999; Jolly 2006; Goodman *et al.* 2006; LaFleur and Gould 2009); however, populations cannot survive in completely degraded habitats or under extreme hunting pressure, the two main threats which have decimated *L. catta* populations throughout its geographic range. Given the current situation of ring-tailed lemurs in the wild, and the enormity of threats that these populations face daily, the question arises: Will we, in the next decade or two, lose the most recognized and iconic of all the lemur species?

Acknowledgments

We thank the Département des Eaux et Forêts, Madagascar, Madagascar National Parks, Community Associations Anja, Sakaviro, FI.MI.VA, Antokinihoavy-Andranobe, and Tantely for granting research permission, and to GERP (Groupe d'étude et de recherche sur les primates de Madagascar) for logistical assistance. L. Gould is grateful to the following for their much appreciated research assistance at the south-central sites: P. Andrianomena, Daniel and Raboary (Tsaranoro), S. Rasoanomenjanahary, J. S. Weir, J. N. Rabialahy. We also thank the following individuals for providing information in the form of personal communications: I. A. J. Youssouf, B. P. Semel, C. Foulon, E. A. Kelley, R. J. Lewis, B. Ferguson, and M. Malone. Funding for the population research at the south-central sites was provided by grants to LG from Conservation International's Primate Action Fund and the University of Victoria (IRG program).

Literature Cited

- Actman, J. 2016. Why you shouldn't share that cute lemur video. Wildlife Watch, National Geographic. 26 April 2016. Website: https://news.mongabay.com/2013/12/madagascars-most-famous-lemur-facing-big-threats. Accessed 9 September 2016.
- Andriaholinirina, N. et al. 2014. Lemur catta. The IUCN Red List of Threatened Species 2014: e.T11496A62260437.
 http://dx.doi.org/10.2305/IUCN.UK.2014-2.RLTS. T11496A62260437.en>. Downloaded on 09 September 2016.
- Blanc-Pamard, C. 2009. The Mikea Forest under threat (southwest Madagascar): how public policy leads to conflicting territories. *Field Actions Science Reports* [Online], Vol. 3. Website: http://factsreports.revues.org/341>. Accessed: 11 October 2012.
- Bodin, O., M. Tengo, A. Norman, J. Lundberg and T. Elmqvist. 2006. The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. *Ecol. Applic.* 16: 440–451.
- Bucht, K. R. 2011. Local Viewpoints on Conservation and Development at Malio, Andohahela National Park, Madagascar. Honors Thesis, Oregon State University, Corvallis, OR.
- Cameron, A. and L. Gould. 2013. Fragment adaptive behavioral strategies and inter-site variation in the ring-tailed lemur (*Lemur catta*) at Anja Special Reserve and the Tsaranoro Valley, south-central Madagascar. In: *Primates in Fragments: Complexity and Resilience*, L. Marsh and C. Chapman (eds.), pp.227–243. Springer, New York.
- Caravel Energy Limited. 2013. Behaza Oil Project. Website: http://www.antaresmining.com.au/BehazaOilProject.html/>. Accessed: 4 August 2014.
- Clarke, T. A., O. Gray, L. Gould and A. S. Burrell. 2015. Genetic diversity of the ring-tailed lemur (*Lemur catta*) in south-central Madagascar. *Folia Primatol.* 86: 76–84.
- Davies, N. and C. Schwitzer. 2013. Lemur conservation status review: an overview of the lemur red-listing results, 2012.
 In: Lemurs of Madagascar. A Strategy for Their Conservation 2013–2016, C. Schwitzer, R. A. Mittermeier, N.

Davies, S. Johnson, J. Ratsimbazafy, J. Razafindramanana, E. E. Louis Jr. and S. Rajaobelina (eds.). pp.13–52. IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation Bristol, UK, and Conservation International, Arlington VA.

- Dolch, R., R. Ratsisetraina, M. Markolf, T. Ratolojanahary, H. Rakotonirina, E. E. Louis Jr. and Wendenbaum, E. 2012. Assessment of lemur diversity in the Makay massif. *Lemur News* 16: 48–53.
- Elmqvist, T., M. Pykkonen, M. Tengo, F. Rakotondrasoa, E. Rabakonandrianina and C. Radimilahy. 2007. Patterns of loss and regeneration of the tropical dry forest in Madagascar: the social institutional context. *PLoS One* 2(5): e402.
- Emmett D. A., E. Fanning and A. Olsson (eds.). 2003. Sept Lacs Region: Wetland Biodiversity and Resource Use Summary. Frontier-Madagascar. Environmental Research Report 7. Society for Environmental Exploration, UK, and the University of Toliara and Institute of Marine Sciences, Madagascar.
- Environmental Justice Atlas. 2015. WTR Ranobe Forest Mining, Madagascar. Website: https://ejatlas.org/con-flict/wtr-ranobe-forest-mining-madagascar. Accessed: 4 August 2015.
- Fenn, M. 2003. The spiny forest ecoregion. In: A Natural History of Madagascar, S. Goodman and J. Benstead (eds.), pp.1525–1530. University of Chicago Press, Chicago, IL.
- Foulon, C., L. Dimilahy, P. Mhia, O. Rahanitriniaina, V. Andrianarimalala, R. Fenomanana, J. Randrianady, M. Ratovoloala, C. Sehenomalala, A. Walker-Bolton, R. Taharisoa, F. Rafenoarisoa, J. Soppelsa, T. Randrianirina, D. Trapon and F. N. Ravahatramananjarasoa. 2015. *Livret de Recensement 2015:* Lemur catta. Rèserve Privèe de Berenty, Madagascar.
- Furrer, R. D. and G. Pasinelli. 2016. Empirical evidence for source-sink populations: a review on occurrence, assessments and implications. *Biol. Rev.* 91: 782–795.
- Gardner, C. J., E. Fanning, H. Thomas and D. Kidney. 2009. The lemur diversity of the Fiherenana-Manombo Complex, southwest Madagascar. *Madagascar Conserv. Develop.* 4: 38–43.
- Gardner, C. J. and Z. G. Davies. 2014. Rural bushmeat consumption within multiple-use protected areas: qualitative evidence from southwest Madagascar. *Hum. Ecol.* 42: 21–34.
- Goodman, S. M. and O. Langrand. 1996. A high mountain population of the ring-tailed lemur *Lemur catta* on the Andringitra Massif, Madagascar. *Oryx* 30: 259–268.
- Goodman, S. M., S. V. Radotoarisoa and L. Wilm. 2006. The distribution and biogeography of the ring-tailed lemur (*Lemur catta*). In: *Ringtailed Lemur Biology:* Lemur catta *in Madagascar*, A. Jolly, R. W. Sussman, N. Koyama and H. Rasamimanana (eds.), pp.3–15. Springer, New York.
- Gould, L. 2006. *Lemur catta* ecology: What we know and what we need to know. In: *Lemurs: Ecology and Adaptation*. L.

Gould and M. L. Sauther (eds.), pp.255–274. Springer, New York.

- Gould, L. and P. Andrianomena. 2015. Ring-tailed lemurs (*Lemur catta*), forest fragments, and community-level conservation in south-central Madagascar. *Primate Conserv*. (29): 67–73.
- Gould, L. and D. N. Gabriel. 2015. Wet and dry season diets of the endangered *Lemur catta* (ring-tailed lemur) in two mountainous rocky outcrop forest fragments in southcentral Madagascar. *Afr. J. Ecol.* 53: 320–330.
- Gould, L., R. W. Sussman and M. L. Sauther. 1999. Natural disasters and primate populations: the effects of a twoyear drought on a naturally occurring population of ringtailed lemurs in southwestern Madagascar. *Int. J. Primatol.* 20: 69–84.
- Gould, L., M. Power, N. Ellwanger and H. Rambeloarivony. 2011. Feeding behavior and nutrient intake in spinyforest dwelling ring-tailed lemurs (*Lemur catta*) during early gestation and early to mid-lactation periods: compensating in a harsh environment. *Am. J. Phys. Anthropol.* 145: 469–479.
- Gould, L., E. A. Kelley and M. LaFleur. 2015. Reproductive female feeding strategies in spiny-forest dwelling *Lemur catta* in southern and southwestern Madagascar: how do females meet the challenges of reproduction in this harsh habitat? *Folia Primatol*. Special issue: *Lemur catta*: A species re-imagined, M. Sauther, F. Cuozzo, K. A. I. Nekaris, L. Gould, and T. O'Mara (eds.). 86: 16–24.
- Harper, G. J., M. K. Steininger, J. Compton, D. J. Tucker and F. Hawkins. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environ. Conserv.* 34: 324–333.
- Hill, W. C. O. 1953. *Primates. Comparative Anatomy and Taxonomy I. Strepsirhini.* Edinburgh University Press, Edinburgh.
- Huff, A. 2016. Black Sands, Green Plans and Conflict: Structural Adjustment, Sectoral Reforms and the Mining-Conservation-Conflict. Assessing and Mitigating Violence: Assessment report #183.Institute of Development Studies, Brighton, UK.
- Irwin, M., K. E. Samonds and J. L. Raharison. 2001. A biological inventory of the lemur community of Réserve Spéciale de Kalambatritra, south-central Madagascar. *Lemur News* 6: 24–28.
- Jolly, A., N. Koyama, H. Rasamimananana, H. Crowley and G. Williams. 2006. Berenty Reserve: a research site in southern Madagascar. In: *Ringtailed Lemur Biology:* Lemur catta *in Madagascar*, A. Jolly, R. W. Sussman, N. Koyama and H. Rasamimanana (eds.), pp.32–42. Springer, New York.
- Kelley, E. A., R. W. Sussman and K. M. Muldoon. 2007. The status of lemur species at Antserananomby: an update. *Primate Conserv.* (22): 71–77.
- Kelley, E. A. 2011. *Lemur catta* in the Region of Cap Sainte-Marie, Madagascar: Introduced Cacti, Xerophytic

Gould and Sauther

Didiereaceae-*Euphorbia* bush, and tombs. PhD dissertation, Washington University, St. Louis, MO.

- Kelley, E. A. 2013. The ranging behavior of *Lemur catta* in the region of Cap Sainte-Marie, Madagascar. *Am. J. Phys. Anthropol.* 150: 122–132.
- LaFleur, M. 2012. Ecology of Ring-tailed Lemurs (*Lemur catta*) at the Tsimanamptesotsa National Park, Madagascar: Implications for Female Dominance and the Evolution of Lemur Traits. PhD dissertation, University of Colorado, Boulder, CO.
- LaFleur, M. 2013. Madagascar's most famous lemur facing big threats. Website: https://news.mongabay.com/2013/12/madagascars-most-famous-lemur-facing-big-threats. 18 December 2013. Accessed: 9 September 2016.
- LaFleur, M. and L. Gould. 2009. Feeding outside the forest: the importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatol.* 80: 233–246.
- LaFleur, M. and M. L. Sauther. 2015. Seasonal feeding ecology of ring-tailed lemurs: a comparison of spiny and gallery forest habitats. *Folia Primatol.* 86: 25–34.
- LaFleur, M., T. Clarke, L. Giraud, I. A. J. Youssouf, L. Gould and M. Adiba. 2015. Reniala Lemur Rescue Center for ringtailed lemurs in Madagascar. *Lemur News* 19: 11–16.
- Lemur Conservation Network. 2015. Ranobe: Madagascar's Forgotten Forest. Website: http://lemurconservation-network.org/ranobe-madagascars-forgotten-forest/. Accessed: 4 August 2015.
- Madagascar Biodiversity Fund. Undated. Andohahela and its ecosystem. Website: http://www.fapbm.org/biodi-versity/andohahela-and-its-ecosystem. Accessed: 11 November 2016.
- Madagascar, MNP. 2015. Parc National Isalo. Madagascar National Parks (MNP). Website: http://www.parcs-madagascar.com/aire-protégée/parc-national-isalo. Accessed: 9 September 2016.
- Madonline. 2014. Préserver la forêt des Sept Lacs. Website: <<u>http://www.madonline.com/preserver-la-foret-des-sept-lacs/></u>. Accessed: 15 August 2015.
- Mahamaro, T. H. 2012. Estimation des populations de lemuriens à Ifotaka par differentes methods. Memoire de fin d'études, Centre Écologique de Libanona, Gestion de l'environnement au service de development, Madagascar.
- Malone, M., J. B. Ramanamanjato, F. Randriatafika, and G. Donati. 2013. Habitat structure and grey mouse lemur (*Microcebus murinus*) abundance in the transitional littoral forest of Petriky, southeast Madagascar. *Lemur News* 17: 22–26.
- ONE, DGF, FTM, MNP and CI. 2013a. Evolution de la Couverture de forêts naturelles à Madagascar / Change in Natural Forest Cover 2005–2010. Rapport. Office National pour l'Environnement (ONE), Direction Générale des Forêts (DGF), Madagascar National Parks (MNP), Foiben-Taosarintanin'i Madagasikara (FTM),

and Conservation International (CI), Antananarivo, Madagascar. 42pp.

- ONE, DGF, FTM, MNP and CI. 2013b. Changement de la Couverture de forêts naturelles à Madagascar / Change in Natural Forest Cover 1990–2000–2005–2010. Map. Office National pour l'Environnement (ONE), Direction Générale des Forêts (DGF), Madagascar National Parks (MNP), Foiben-Taosarintanin'i Madagasikara (FTM), and Conservation International (CI), Antananarivo, Madagascar.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652-661.
- Raharivololona, B.M. and V. Ranaivosoa. 2000. Suivi écologique des Lémuriens diurnes dans le Parc National d'Andohahela à Fort-Dauphin. *Lemur News* 5: 8–11.
- Ranaivonasy, J., J. Ratsirarson, N. Rasamimanana and E. Ramahatratra. 2016. Dynamique de la couverture forestière dans la Réserve Spéciale de Bezà Mahafaly et ses environs, J. Ranaivonasy, J. Ratsirarson and A. F. Richard (eds.). *Malagasy Nature* 10: 15–24.
- Rasoarimanana, J. 2005. Suivi des lémuriens diurnes dans le Parc Nationale d'Andohahela. *Lemur News* 10: 27–29.
- Rasolofoharivelo, T., L. H. F. Rakotonirina and T. King. 2013.
 Kalambatritra Massif. In: *Lemurs of Madagascar. A Strategy for Their Conservation 2013–2016*, C. Schwitzer, R. A. Mittermeier, N. Davies, S. Johnson, J. Ratsimbazafy, J. Razafindramanana, E. E. Louis Jr. and S. Rajaobelina (eds.), pp.101–103. IUCN SSC Primate Specialist Group, Bristol Conservation Foundation, Bristol, UK, and Conservation International, Arlington, VA.
- Ravelohasindrazana, L. A. L. 2013. Étude de la population *Lemur catta* de la NAP Tsinjoriake site d'Antsifotse. Mémoire de fin d'étude en vue de l'obtention du diplôme de Licence Professionnelle en Biodiversité et Environnement (5^e promotion). Option: Biologie Animale. Faculté de Science, Université de Toliara, Toliara, Madagascar.
- Ravoavy, J. F. 2013. Étude de la population de *Lemur catta* (Maki), dans la Nouvelle Aire Protégée Tsinjoriaky, Région Sud-Ouest de Madagascar. Mémoire en vue de l'obtention du Diplôme de Licence Professionnelle en Biodiversité et Environnement. Faculté de Science, Université de Toliara, Toliara, Madagascar.
- Razafindramanana, J. 2011. Behavioural Ecology of Sympatric Lemur Species *Lemur catta* and *Eulemur* sp. in Forest Fragments, South-eastern Madagascar. PhD Dissertation, Oxford Brookes University, Oxford, UK.
- Reuter, K., H. Gilles, A. Wills and B. J. Sewall. 2016. Live capture and ownership of lemurs in Madagascar: extent and conservation implications. *Oryx* 50: 344–354.
- Sauther, M. L. 2014. Should I stay or should I go now? How social, developmental and ecological factors influence patterns of male and female dispersal in a wild ring-tailed lemur population. *Am. J. Phys. Anthropol.* 153 (S58): 229.

- Sauther, M. L., R. W. Sussman and L. Gould. 1999. The socioecology of the ring-tailed lemur: thirty-five years of research. *Evol. Anthropol.* 8: 120–132.
- Sauther, M. L., F. P. Cuozzo, I. A. J. Youssouf, K. D. Fish, M. LaFleur, L. A. L. Ravelohasindrazana and J. F. Ravoavy. 2013. Limestone cliff-face and cave use by wild ringtailed lemurs (*Lemur catta*) in southwestern Madagascar. *Madagascar Conserv. Develop.* 8: 73–80.
- Sauther, M. L., L. Gould, F. P. Cuozzo and M. T. O'Mara. 2015. Ring-tailed lemurs: a species re-imagined. *Folia Primatol.* 86: 5–13.
- Seddon, N., J. Tobias, J. W. Yount, J. R. Ramanampamonjy, S. Butchart and H. Randrianizahana. 2000. Conservation issues and priorities in the Mikea Forest of south-west Madagascar. *Oryx* 34: 287–304.
- Semel, B.P. and B. Ferguson. 2013. Ring-tailed lemurs (*Lemur catta*) using cliffs as sleeping sites. *Lemur News* 17: 4–6.
- Sterman, S. 2012. Vohipary: A Biodiversity Reconnaissance Mission. SIT Madagascar: Biodiversity and Natural Resource Management Program Report, Yale Center for International and Professional Experience, New Haven, CT.
- Sussman, R. W. 1972. An Ecological Study of Two Madagascan Primates: *Lemur fulvus rufus* Audebert and *Lemur catta* Linnaeus. PhD dissertation, Duke University, Durham, NC.
- Sussman, R. W., G. M. Green, I. Porton, O. L. Andrianasolondaibe and J. A. Ratsirarson. 2003. Survey of the habitat of *Lemur catta* in southwestern and southern Madagascar. *Primate Conserv.* (19): 32–57.
- Sussman, R. W., S. Sweeny, G. M. Green, I. Porton, O. L. Andrinanasolondraibe and J. A. Ratsirarson. 2006. A preliminary estimate of *Lemur catta* population density using satellite imagery. In: *Ringtailed Lemur Biology:* Lemur catta *in Madagascar*, A. Jolly, R. W. Sussman, N. Koyama and H. Rasamimanana (eds.), pp.16–31. Springer, New York.
- Sussman, R. W., A. F. Richard, J. Ratsirarson, M. S. Sauther, D. Brockman, L. Gould, R. Lawler and F. Cuozzo. 2012. Beza Mahafaly Special Reserve: long-term research on lemurs in southwestern Madagascar. In: *Long-term Field studies of Primates*, P. M. Kappeler and D. Watts (eds.), pp.45–66. Springer, New York.
- Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.
- Tengo, M. and J. von Heland. 2014. Trees and tree-planting in southern Madagascar: sacredness and remembrance. In: *Greening in the Red Zone: Disaster, Resilience and Community Greening*, K. G. Tidball and M. E. Krasny (eds.), pp.333–338. Springer, New York.
- Tilghman, L., M. Baker and S. Dickinson DeLeon. 2005. Artisanal sapphire mining in Madagascar: environmental and social impacts. *University of Vermont Gemecology Reports*, Burlington, VT. 54pp. URL: /.

- Travel Madagascar. Undated. Pic d'Ivohibe Special Reserve. Website: http://www.travelmadagascar.org/PARKS/Pic-Ivohibe-Reserve.html. Accessed: 9 September 2016.
- Wendenbaum, E., A. Laudisot and J. M, Bichain. 2013. Makay. In: Lemurs of Madagascar. A Strategy for Their Conservation 2013–2016, C. Schwitzer, R. A. Mittermeier, N. Davies, S. Johnson, J. Ratsimbazafy, J. Razafindramanana, E. E. Louis Jr. and S. Rajaobelina (eds.), pp.109–112. IUCN SSC Primate Specialist Group, Bristol Conservation Foundation, Bristol, UK, and Conservation International, Arlington, VA.
- Zinner, D., J. Ostner, A. Dill, L. Razafimanantsoa and R. Rasoloarison. 2001. Results of a reconnaissance expedition in the western dry forests between Morondava and Morombe. *Lemur News* 6: 16–18.

Authors' addresses:

Lisa Gould, Department of Anthropology, University of Victoria, 3800 Finnerty Road, Victoria, BC V8P 5C2, Canada, and Michelle L. Sauther, Department of Anthropology, University of Colorado, Boulder, CO, USA. *Corresponding author:* E-mail: <Lgould@uvic.ca>.

Received for publication: 5 September 2016 Revised: 11 November 2016