Short Communication

Folia Primatol 2016;87:320–330
DOI: 10.1159/000455121

Received: August 29, 2016
Accepted after revision: December 14, 2016
Published online: January 13, 2017

Rapid Decrease in Populations of Wild Ring-Tailed Lemurs (*Lemur catta*) in Madagascar

Marni LaFleur[a] Tara A. Clarke[b] Kim Reuter[c] Toby Schaeffer[d]

[a]Department of Anthropology, University of California San Diego, La Jolla, CA, and [b]Evolutionary Anthropology Department, Duke University, Durham, NC, USA; [c]Africa Field Division, Conservation International, and [d]Independent Consultant (pro bono), Nairobi, Kenya

Keywords
Ring-tailed lemur · Madagascar · Extinction · Bushmeat · Pet trade · Population decline · *Lemur catta*

Abstract
Lemurs are the most threatened group of mammals on earth. *Lemur catta* (ring-tailed lemur) represents one of the most iconic lemur species and faces numerous anthropogenic threats in the wild. In this study, we present population estimates from 32 sites across the range of *L. catta*, collected from primary and secondary data sources, to assess the number of ring-tailed lemurs left in the wild. We estimate that there are approximately 2,220 individual *L. catta* remaining in the 32 sites considered. We note local extinctions of populations of *L. catta* in at least 12 of the 32 sites examined, and that significantly more extinctions occurred in areas without some form of protection. This decrease in extant populations could represent a decrease of more than 95% of all ring-tailed lemurs in Madagascar since the year 2000. While these results should be considered preliminary, we stress the rapid decline of the species and note that habitat loss, bushmeat hunting and the illegal pet trade are driving populations to local extinction. Based on the data presented here, urgent and immediate funding and conservation action are crucial to ensure the viability of the remaining wild populations of ring-tailed lemurs.

Introduction

Lemurs are the most threatened group of mammals on earth and are endemic to Madagascar, a biodiversity hotspot [Schwitzer et al., 2014]. Lemurs face numerous threats, including habitat loss due to deforestation and climate change [Brown and

KARGER
E-Mail karger@karger.com
www.karger.com/fpr

0015–5713/17/0875–0320$39.50/0

Marni LaFleur
Department of Anthropology
University of California San Diego
Campus Box 0532, La Jolla, CA 92093 (USA)
E-Mail marni.lafleur@gmail.com

Yoder 2015], hunting [Schwitzer et al., 2014], and the illegal pet trade [Reuter et al., 2016]. Lemurs have been described as "the single highest primate conservation priority in the world" [Schwitzer et al., 2013, p. 5].

Ring-tailed lemurs (*Lemur catta*) are a flagship species for conservation, and are, perhaps, Madagascar's best-known primate. These lemurs are characterized by their behavioural flexibility, in that their sociality (e.g., dominance/rank relationships, aggression) and activity budgets vary according to environmental conditions [Sauther et al., 1999], and ecological plasticity, in that they can inhabit a plethora of habitat types [Goodman et al., 2006] and rebound from environmental perturbations [Gould et al., 1999]. The first large-scale population estimates of wild ring-tailed lemur habitats and individuals estimated a 9.5% habitat and 20% population decrease between 1985 and 2000 (population estimated at 751,251 in the year 2000 [Sussman et al., 2006]). Since then, census attempts of specific sites have continued [e.g., Kelley, 2013; Dimilahy et al., 2015; Gould and Andrianomena, 2015], yielding evidence of localized ring-tailed lemur extinctions [Gardner and Davies, 2014] and a suspected population decline rate of over 50% over a 3-generation period [Andriaholinirina et al., 2014].

Population declines of *L. catta* are driven by various threats. Ring-tailed lemurs represent 28% of individuals kept as in-country illegal pets [Reuter and Schaefer, 2016], and are sometimes killed and consumed by their human owners [Reuter and Schaefer, in press]. This species also faces direct hunting pressure [e.g., Goodman 2003], significant habitat loss [Brinkmann et al., 2014], and population declines resulting from the effects of climate change [Brown and Yoder, 2015]. As a result, *L. catta* is now restricted to isolated fragments [Sussman et al., 2003] with relatively low population densities [Kelley 2013; Andriaholinirina et al., 2014; Gould and Andrianomena, 2015], and its survival in the wild at most locations remains perilous [but see Dimilahy et al., 2015].

In this study, we present a population estimate for ring-tailed lemurs across 32 locations within their natural and historical range across south-western Madagascar. Moreover, we discuss the consequences of our findings and propose next steps to ensure the long-term viability of remaining wild populations.

Methods

Estimating Population Numbers at Known Sites

We assessed the status of populations of *L. catta* at 32 locations where they are known to occur (Fig. 1; Table 1). Similar to a census of chimpanzees (*Pan troglodytes*) by Plumptre and Cox [2006], we collected primary and secondary data regarding the largest known and/or protected habitat fragments in which *L. catta* is found to estimate the total number of individuals left in the wild. *L. catta* is found at locations outside of these 32 known sites [Goodman et al., 2006, map approx. 100 records of wild populations of *L. catta*); however, these 32 sites likely comprise the largest remaining populations of *L. catta*, as many of the previously mentioned "known" sites are now deforested or devoid of animals [Sussman et al., 2006; Gardner and Davies, 2014].

To assess the status of populations of *L. catta* at these 32 sites, we used a mixture of methods: in-person site visits (M.L. and T.A.C.), personal communication with other researchers, and information gleaned from the published literature (Table 1). We could not visit all 32 field sites due to time and budget limitations; for in-person site surveys, we prioritized locations where previous researchers suggested that populations of *L. catta* were under significant extraction pressure [e.g., Kirindy Mitea Sud hunting pressure, Goodman, 2003; Andohahela hunting pressure, Siers, 2007].

For in-person site surveys (n = 10 sites, Table 1), M.L. and T.A.C. spent a minimum of 2 days at each site in June-August 2016 and used rapid assessment methods [Gilles and Reuter,

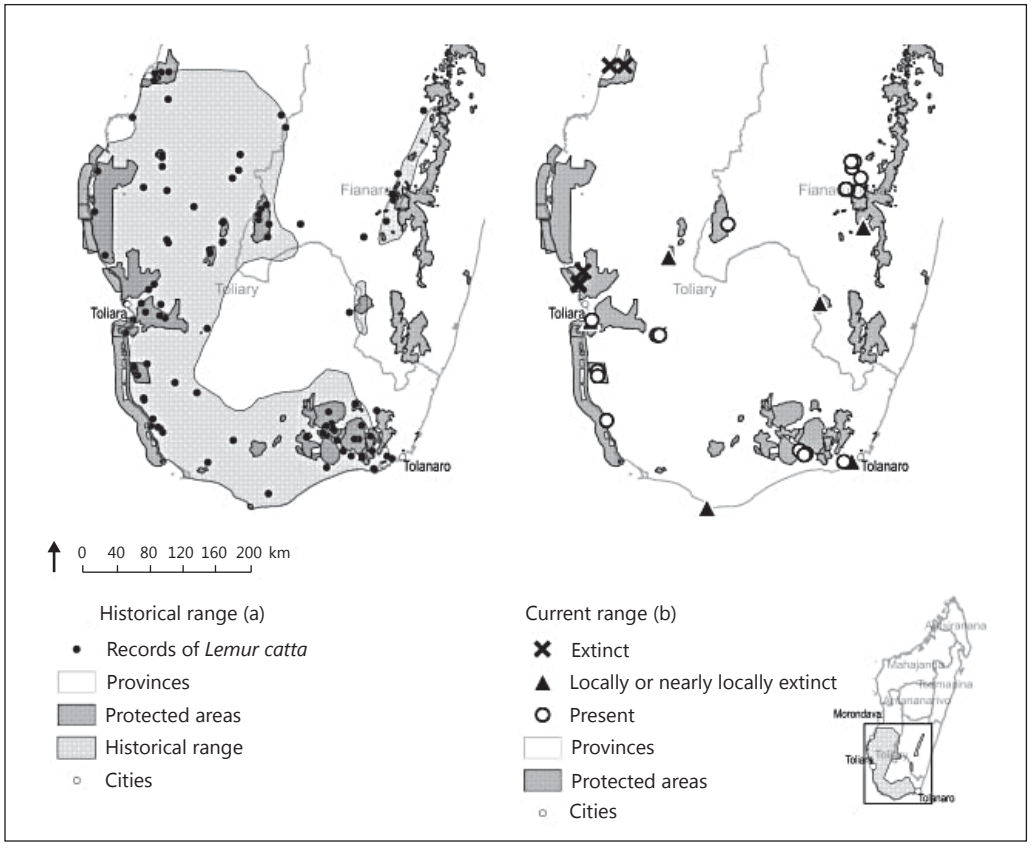

Fig. 1. Historical range (**a**) and estimated current range (**b**) for *L. catta*, including areas where populations are present, locally extinct, or likely or nearly locally extinct. **a** Data are from Goodman et al. [2006] and Andriaholinirina et al. [2014]. **b** References are available from Table 1.

2014] to confirm or fail to confirm the presence of *L. catta*. Since we aimed to confirm the presence of ring-tailed lemurs in the locations visited, we took steps to increase the chances of detecting animals. These included speaking to local officials and villagers in order to understand where animals had been seen in the recent past, or where ring-tailed lemur troops' sleep sites or frequently used trees may be located. Once target areas were identified, we then walked on both forest trails and off-trail locations for between 5 and 12 km/day, while trying to detect the presence of ring-tailed lemurs. Confirmation of the presence of *L. catta* included hearing calls or observing animal(s), or indirect indicators of presence such as seeing footprints, spur markings on vegetation, bite marks on plants/foods, and/or presence of faeces. Indirect indicators of animal presence are reliable when efforts are standardized and consistent [Macdonald et al., 1999], and can be used to detect population changes in wildlife [Gese, 2001]. At all sites where the presence of *L. catta* could not be confirmed, M.L. and T.A.C. spoke with park managers, tour guides, and/or local community members to understand when and how many *L. catta* had last been seen at that site, and whether the animals had faced any known threats in the past. At 7 out of 10 sites, M.L. and T.A.C. were unable to confirm the presence of *L. catta* and therefore consider these populations to be locally extinct unless otherwise noted (Table 1). At the remaining 3 sites (Isalo

Folia Primatol 2016;87:320–330
DOI: 10.1159/000455121

Table 1. Locations of known populations of *L. catta* included in the scope of this paper

Location name	Coordinates	Protected status	Population category	Number of animals	Size of forest fragment or protected area[a], km^2	Year of assess-ment	Source of information	Days of rapid sampling	Citation (most recent known)
Ambatotsirongorongo Forest	25°04.70′ S, 46°47.24′ E	Protected area	Present	50	0.25	2010	Literature	–	Razafindramanana, 2011
Ambinany (Berenty region)	24°59.53′ S, 46°18.07′ E	Private reserve	Present	65	–	2015	Literature	–	Dimilahy et al., 2015
Andohahela	24°08.72′ S, 43°49.74′ E	National park	Present*	82	760	2000	Literature	–	Moniac and Heitman, 2007
Andranobe (Ambolavoa region)	21°57.78′ S, 46°56.73′ E	Community-level association	Present	36	0.381	2013	Literature	–	Gould and Andrianomena, 2015
Andringitra	22°06.76′ S, 46°55.38′ E	National park	Present	106	31,134	1995	Literature	–	Rakotoarisoa, 1999
Anja Miray (Ambalovoa region)	21°51.12′ S, 46°50.40′ E	Community-level association	Present	210	0.36	2013	Literature	–	Gould and Andrianomena, 2015
Anjapolo (Berenty region)	24°57.66′ S, 46°15.06′ E	Private reserve	Present	151	–	2015	Literature	–	Dimilahy et al., 2015
Bealoka (Berenty region)	25°00.59′ S, 46°18.51′ E	Private reserve	Present*	163	1	2009	Literature	–	Dimilahy et al., 2015; Sussman et al., 2006
Berenty (Berenty region)	24°59.88′ S, 46°19.87′ E	Private reserve	Present	562	2	2010	Literature	–	Dimilahy et al., 2015
Beza Mahafaly Parcel 1	23°42.00′ S, 44°32.33′ E	Special reserve	Present	124	0.8	2014	Pers. commun.	–	Sauther, pers. commun.
Beza Mahafaly Parcel 2	23°42.00′ S, 44°34.33′ E	Special reserve	Present	205	5.2	2014	Pers. commun.	–	Sauther, pers. commun.
Cap Sainte-Marie[b]	25°35.75′ S, 45°08.35′ E	Special reserve	Locally or nearly locally extinct*	50	0.18	2008	Literature	–	Kelley, 2013
Chameleon (Tsaranoro Valley)	Unknown	Community-level association	Present	28	0.08	2013	Literature	–	Gould and Andrianomena, 2015

Table 1 (continued)

Location name	Coordinates	Protected status	Population category	Number of animals	Size of forest fragment or protected area[a], km^2	Year of assessment	Source of information	Days of rapid sampling	Citation (most recent known)
Ifaty	23°08.71′ S, 43°36.95′ E	Unprotected	Extinct*	0	–	2015; 2016	Literature; pers. observation	–, 2	LaFleur et al., 2015
Isalo (Maki canyon)[c]	22°29.26′ S, 45°22.73′ E	National park	Present	118	0.5	1995; 2016	Literature; pers. observation	–, 1	Hawkins, 1999
Isalo (Namaza circuit)[c]	23°31.82′ S, 43°46.01′ E	National park	Present		–	1995; 2016	Literature; pers. observation	–, 1	Hawkins, 1999
Kalambatritra	23°20.50′ S, 46°28.66′ E	Special reserve	Locally or nearly locally extinct*	0	282.55	2005	Literature	–	Irwin et al., 2005[d]
Kirindy Mitea	20°44.38′ S, 44°10.32′ E	National park	Extinct*	0	722	2016	Pers. commun.; pers. observation	–, 1	Lewis B., pers. commun.; Goodman, 2003
Kirindy Mitea de sud	20°44.23′ S, 44°00.07′ E	Unprotected	Extinct*	0	–	2016	Pers. observation	–, 2	Goodman, 2003
Mangily (Reniala Private Reserve)	23°07.59′ S, 43°36.80′ E	Unprotected	Extinct*	0	0.6	2015	Literature; pers. observation	–, 2	LaFleur et al., 2015; Gardner and Davies, 2014
Marody (Tsaranoro Valley)	22°05.57′ S, 46°47.65′ E	Community-level association	Present	15	0.028	2013	Literature	–	Gould and Andrianomena, 2015
Petriky	25°04.31′ S, 46°53.10′ E	Unprotected	Locally or nearly locally extinct*	4	11.8	2012	Literature	–	Malone et al., 2013
Pic d'Ivohibe	22°30.00′ S, 46°59.00′ E	Special reserve	Locally or nearly locally extinct*	0	34.5	2005	Literature	–	Irwin et al., 2004[d]
PK 32-Ranobe	22°59.82′ S, 43°40.20′ E	Protected area	Extinct*	0	200.46	2010	Literature	–	Gardner and Davies, 2014
Sakarivo Miray (Ambolavoa region)	21°47.01′ S, 46°52.07′ E	Community-level association	Present	30	0.142	2013	Literature	–	Gould and Andrianomena, 2015
Samisoramy (Ambalavoa region)	21°47.18′ S, 24°49.83′ E	Community-level association	Present	21	0.203	2013	Literature	–	Gould and Andrianomena, 2015

Folia Primatol 2016;87:320–330
DOI: 10.1159/000455121

Table 1 (continued)

Location name	Coordinates	Protected status	Population category	Number of animals	Size of forest fragment or protected area[a], km^2	Year of assessment	Source of information	Days of rapid sampling	Citation (most recent known)
Tsaranoro (Tsaranoro Valley)	22°05.18′ S, 46°46.32′ E	Community-level associations	Present	78	0.46	2013	Literature	–	Gould and Andrianomena, 2015
Tsimanampetsotsa (northern boundary)	24°05.40′ S, 43°49.80′ E	National park	Present	67	–	2016	Pers. observation	10 (including research for a larger, ongoing project on ring-tailed lemur ecology)	
Tsimanampetsotsa (southern boundary)	24°37.98′ S, 43°55.98′ E	National park	Present	40	–	2015	Pers. commun.	–	Louis E.E., pers. commun.
Tsinjoriake (Moringa circuit)[b]	23°31.31′ S, 43°45.28′ E	Protected area	Locally or nearly locally extinct*	5	50	2016	Pers. commun.; pers. observation	–, 3	Youssouf J., pers. commun.
Tsinjoriake (southern mangrove area)	23°32.18′ S, 43°44.68′ E	Protected area	Locally or nearly locally extinct*	0	–	2016	Pers. observation	–, 3	
Zombitse-Vohibasia[e]	22°50.50′ S, 44°40.91′ E	National park	Locally or nearly locally extinct*	10	0.36	2016	Pers. commun.; pers. observation	–, 2	Madagascar National Parks, pers. commun.; Siers, 2007
Total				2,220					

An asterisk indicates known exploitation pressures (e.g., hunting) at the location against *L. catta*. "Personal observation" indicates that we collected data during a site visit in 2016.

[a] These area estimates should be interpreted with caution as they were often not reported alongside density estimates but have been extracted from various, publicly available documents.

[b] Kelley [2013] reports a range of 35–50 individual ring-tailed lemurs at Cap Sainte-Marie. Similarly, although we failed to detect the presence of animals, a student of Dr. Youssouff reported seeing a range of 4–5 animals in Tsinjoriake (Moringa circuit) in August 2016. For the purposes of this paper, we used the larger value for the number of individual lemurs at both sites.

[c] We confirmed the presence of ring-tailed lemurs at Isalo but were unable to sample all known groups. We thus used data from Hawkins [1999] to estimate the total number of animals. Hawkins [1999] does not differentiate between the 2 populations of ring-tailed lemurs present, and thus we cite 1 value here for all of Isalo.

[d] Irwin et al. [2004] conducted extensive censuses at Pic d'Ivohibe and Kalambatritra. Their censuses do not report the presence of ring-tailed lemurs, and here we use these data to infer the absence of the species.

[e] We failed to detect animals, but the Madagascar National Parks ecological monitoring team reported the presence of 10 animals in March 2016 (3 months previously).

Maki canyon, Namaza circuit, Tsimanampesotse northern boundary), we estimated how many *L. catta* were likely present by counting animals in known groups. More specifically, at Isalo (Maki canyon), we walked a circuit until we encountered ring-tailed lemur groups and then followed the animals for a minimum of 1 h, in order to ascertain how many animals were travelling with the group. At Isalo (Namaza circuit), we remained in a tourist picnic spot, and when ring-tailed lemur groups came through we monitored/followed individuals to determine the group size and identity. At Tsimanampesotse, we monitored known groups and detailed any intergroup encounters with neighbouring/unknown groups. For sites not visited in person ($n = 22$), we collected data from the literature and from colleagues who had visited these sites (Table 1).

Given the variations in sample size, methodological approach, sampling effort, and date of assessment, our compiled data largely violate assumptions of parametric and non-parametric statistics. Thus, the majority of our analyses are descriptive in nature. We present the mean, range, and median numbers of ring-tailed lemurs present at each of the 32 study sites, and compare the likelihood of local extinction between protected and unprotected areas (Fisher exact test, $p = 0.05$). We recognize that the data presented here are limited and must be treated with caution. Both over- and underestimations are possible in the data presented here. Overestimations are possible in the data that were collected several years ago [Gould and Andrianomena, 2015], as animals may no longer be present. Underestimates are also possible in areas where sampling effort has not been sufficient, such as large protected areas without extensive monitoring (i.e., Tsimanampesotse National Park, Isalo National Park). Despite these limitations, the data presented here are still informative in understanding decreasing population trends and the urgent conservation threats faced by ring-tailed lemurs.

Results

Parameters of the Data Set

We sourced data for 84% of the sites ($n = 27$ out of 32) from information made public in 2010 or thereafter (Table 1). Ring-tailed lemurs' historical range covers roughly 100,000 km^2 throughout southern Madagascar, although this generalized estimate includes both habitable (e.g., forested) and uninhabitable (e.g., rivers, cities) areas [Sussman et al., 2006]. The sites assessed here covered the habitable area of approximately 33,208 km^2 (Table 1).

Estimated Population Size across 32 Sites

We estimate the presence/absence and total number of animals remaining at the 32 sites considered in this study. *L. catta* were deemed locally extinct or nearly locally extinct (i.e., we were unable to detect the animals' presence; fewer than 5 animals remaining at last known sighting) in 37.5% of the sites included in this study ($n = 12$ of 32, Table 1). A higher percentage of areas with some form of protection or management status (69% of $n = 29$ sites) had extant ring-tailed lemur populations, when compared to unprotected areas (0% of $n = 3$ sites, Fisher exact test, $n = 32$, $p = 0.0444$, sites with extinct and likely extinct populations grouped together).

The sites had an average of 72 ± 110 (mean ± SD; range: 0–562; median 36) individuals of *L. catta* per site (Table 1). In 2 instances the numbers of animals were reported as a range including 35–50 individual ring-tailed lemurs at Cap Sainte-Marie [Kelley, 2013] and 4–5 individual ring-tailed lemurs at Tsinjoriake [Youssouff, pers. commun.]. For these 2 instances we included the high estimates of the number of animals present (Table 1). Only 8 of 32 sites had populations of more than 100 individuals (Table 1). Sites with some protection ($n = 28$ sites) had an average of 79 ±

113 individuals, while sites without protection (n = 3 sites) had an average of 3 ± 1 individuals left at the site. From the sum of all sites examined, we estimate that there are approximately 2,220 ring-tailed lemurs remaining in the sites included in this study (Table 1).

Discussion

We estimate that there are 2,220 *L. catta* remaining at the 32 sites included in this study. This estimate may not account for all small forest fragments where ring-tailed lemurs could persist or all possible groups of animals in unmonitored areas of large National Parks (i.e., Tsimanampesoste, Isalo), and thus could underestimate the total number of animals remaining. Alternatively, the estimate could include animals that have been extirpated very recently, and thus be inflated. Given that the previous estimates for individual wild ring-tailed lemurs were 2 orders of magnitude larger (i.e., 751,251 [Sussman et al., 2006]), we are confident that there has been a rapid decrease in the numbers of animals living in the wild in Madagascar. Though we acknowledge that both ours and the population estimates of Sussman et al. [2006] were calculated with caveats, this sharp decline is concerning. Both complete deforestation of land parcels and decline of their lemur inhabitants [e.g., Kelley et al., 2007, Antserananomby Forest] and localized extirpations of ring-tailed lemurs without forest clearing (e.g., Ranobe area [Gardner and Davies, 2014]) have been previously documented. Current and detailed data regarding the numbers of ring-tailed lemurs persisting in all of their habitats are urgently needed to understand fully the dramatic decline in wild ring-tailed lemurs and prevent complete extinction in the wild.

The rapid decline in populations of *L. catta* has implications for conservation of the species. First, we found only 1 site with a population of >500 *L. catta* (Table 1). In Uganda, sites with <500 chimpanzees (*Pan troglodytes*) are of conservation concern as smaller populations are not able to sustain genetic viability in the long term [Plumptre and Cox 2006]. In the case of *L. catta*, Clarke et al. [2015] found that ring-tailed lemur populations with fewer than 500 individuals in the central highlands maintain moderate levels of genetic diversity. These populations, however, are likely exhibiting a time lag response whereby genetic diversity will decrease substantially in the future due to continued population fragmentation and associated impacts [Clarke et al., 2015]. Both the low numbers of individuals at isolated sites (and the individuals' potential inability to find mates), and the consequences of low genetic diversity are problematic for ring-tailed lemurs' long-term survival in the wild. Second, we found that unprotected areas are more likely to experience population extinctions of ring-tailed lemurs. The general effectiveness of protected areas in maintaining species presence has been documented globally [see Naughton-Treves et al., 2005], and within the order Primates [see Pusey et al., 2007], although effective management of protected areas is also necessary, as has been noted for lemur species specifically [Schwitzer et al., 2014]. Madagascar has been plagued with political turmoil, yet even during times of crisis, conservation threats are more significant outside protected areas [Schwitzer et al., 2014]. The combination of higher levels of genetic diversity within larger populations and better survivorship within protected areas suggests that conservation priorities for ring-tailed lemurs should include areas with more animals and established protection (Table 1).

At the global scale, population extinctions are a more sensitive indicator of the loss of biodiversity than species extinctions [Ceballos and Ehrlich, 2002]. Likewise, because *L. catta* is known for its ecological flexibility [Sauther et al., 1999], it could be a proxy for biodiversity loss as its population decline underscores the difficulty that other, less adaptable species have in overcoming a multitude of threats. As a well-known and frequently encountered species (i.e., globally in zoos, and at select popular tourist sites in Madagascar), the overarching perception is that *L. catta* is not globally threatened, nor in imminent threat of extinction. A primate species' prevalence in the media has been associated with the belief that wild populations are stable and not threatened by extinction [Leighty et al., 2015; Nekaris et al., 2016]. This false impression that ring-tailed lemurs are not threatened with extinction could be devastating for the species (and larger communities of biodiversity in Madagascar) as it may impede the ability to secure funding for rapid conservation action. That being said, *L. catta* is currently under consideration for inclusion in the 2016–2018 "World's 25 Most Endangered Primates" listing, which is published bi-annually by the IUCN/SSC Primate Specialist Group [IUCN, 2016]. Inclusion of ring-tailed lemurs in this list will highlight the threats these animals are facing and inform the larger conservation community about the fact that even adaptable, flexible species such as ring-tailed lemurs can experience rapid decline.

Several urgent conservation actions should be considered with regard to protecting *L. catta* from extinction in the wild. First, it has been suggested that primate populations threatened with extinction should be regularly monitored using routine site visits [Plumptre and Cox, 2006]. For *L. catta* this monitoring is especially necessary at sites that have large remaining populations and in areas that are data deficient; a complete site-based census of *L. catta* sites is recommended. Second, long-term genetic viability is greater in populations with more individuals [Plumptre and Cox, 2006]. Since there are likely only 8 ring-tailed lemur populations remaining that have more than 100 individual animals (Table 1), these populations should be targeted for protection in order to maintain genetic diversity of the species. Additionally, reintroduction of captive ring-tailed lemurs, particularly those confiscated from the illegal pet trade [LaFleur et al., 2015] could be used as a mechanism to increase wild genetic diversity and to repopulate forested areas where populations are now extinct. Reintroductions are not without risks however, and comprehensive assessments of both prospective animals and release sites would need to be carried out, as per IUCN reintroduction guidelines [IUCN/SSC, 2013]. Third, live capture for the within-country pet trade poses a significant threat to many lemur species. More than 28,000 lemurs were kept in illegal captivity between 2010 and mid-2013, and of these ring-tailed lemurs were the most prevalent, comprising 28% of reported animals [Reuter et al., 2016]. Information regarding drivers and locations of capture, trade routes, and absolute numbers of ring-tailed lemurs in the illegal pet trade is imperative to future conservation initiatives [Reuter and Schaefer, 2016].

Madagascar is one of the world's poorest countries, and poverty is a significant predictor of extinction for primate species [Estrada, 2013]. The primary threats to ring-tailed lemurs, including deforestation and capture for the bushmeat and pet trades, can each be linked to poverty in that subsistence living depends heavily on natural resource exploitation [Brimont et al., 2015] and that forest products, including lemurs, can be sold to generate income [Gardner and Davis, 2014]. It is critical to link conservation efforts with social and economic development projects, in order to ensure that both Madagascar's human population and wildlife thrive.

Acknowledgements

The authors thank the Government of Madagascar, Ministry of the Environment and Ecology of Forests, Madagascar National Parks, the University of Toliara, and MICET, for their permissions and facilitations of our research. We also wish to thank Lydia Greene and Holly Schneider-Brown for their dedication to forwarding lemur conservation and awareness. Additionally, we thank Dr. Anna Nekaris and 3 anonymous reviewers for their feedback, which significantly improved this paper. Funding was provided by the Margot Marsh Biodiversity Foundation, Margot Marsh Primate Action Fund, Duke University's Arts and Sciences Council: Committee on Faculty Research Grant (awarded to T.A.C.), and Lemur Love Inc. private donors.

Disclosure Statement

We understand *Folia Primatologica*'s declaration of interests and declare that we have no competing interests.

References

Andriaholinirina N, Baden A, Blanco M, Chikhi L, Cooke A, Davies N, Dolch R, Donati G, Ganzhorn J, Golden C, Groeneveld LF, Hapke A, Irwin M, Johnson S, Kappeler P, King T, Lewis R, Louis EE, Markolf M, Mass V, Mittermeier RA, Nichols R, Patel E, Rabarivola CJ, Raharivololona B, Rajaobelina S, Rakotoarisoa G, et al. (2014). *Lemur catta*. The IUCN Red List of Threatened Species 2014: e.T11496A62260437.

Brinkmann K, Noromiarilanto F, Ratovonamana RY, Buerkert A (2014). Deforestation processes in south-western Madagascar over the past 40 years: what can we learn from settlement characteristics? *Agriculture, Ecosystems & Environment* 195: 231–243.

Brimont L, Ezzine-de-Blas D, Karsenty A, Toulon A (2015). Achieving conservation and equity amidst extreme poverty and climate risk: the Makira REDD+ project in Madagascar. *Forests* 6: 748–768.

Brown JL, Yoder AD (2015). Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution* 5: 1131–1142.

Ceballos G, Ehrlich PR (2002). Mammal population losses and the extinction crisis. *Science* 296: 904–907.

Clarke TA, Gray O, Gould L, Burrell AS (2015). Genetic diversity of the ring-tailed lemur (*Lemur catta*) in south-central Madagascar. *Folia Primatologica* 86: 76–84.

Dimilahy L, Foulon C, Mhia P, Rahanitriniaina O, Andrianarimalala V, Fenomanana R, Randrianady J, Ratovolala M, Sehenomalala C, Walker-Bolton A, Tahirisoa R, Rafenoarisoa F, Soppelsa J, Randrianirina T, Trapon D, Ravahatramanan-Jarasoa FN (2015). Livret de recensement 2015 *Lemur catta*, Réserve Privée de Berenty 1936–2015. Unpublished report.

Estrada A (2013). Socioeconomic context of primate conservation: population, poverty, global economic demands and sustainable land use. *American Journal of Primatology* 75: 30–45.

Gardner CJ, Davies ZG (2014). Rural bushmeat consumption within multiple-use protected areas: qualitative evidence from southwest Madagascar. *Human Ecology* 42: 21–34.

Gese EM (2001). Monitoring of terrestrial carnivore populations. USDA National Wildlife Research Center Publication No 576. http://digitalcommons.unl.edu/icwdm_usdanwrc/576.

Gilles H, Reuter KE (2014). The presence of diurnal lemurs and human-lemur interactions within the buffer zone of the Ankarana National Park. *Lemur News* 18: 27–30.

Goodman S (2003). Hunting of wild animals by Sakalava of the Menabe region: a field report from Kirindy-Mite. *Lemur News* 8: 4–6.

Goodman SM, Rakotoarisoa SV, Wilmé L (2006). The distribution and biogeography of the ringtailed lemur (*Lemur catta*) in Madagascar. In *Ringtailed Lemur Biology* (Jolly A, Sussman RW, Koyama N, Rasamimanana H, eds.), pp 3–15. New York, Springer.

Gould L, Andrianomena P (2015). Ring-tailed lemurs (*Lemur catta*), forest fragments, and community-level conservation in south-central Madagascar. *Primate Conservation* 29: 67–73.

Gould L, Sussman RW, Sauther ML (1999). Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *International Journal of Primatology* 20: 69–84.

Hawkins A (1999). The primates of Isalo National Park, Madagascar. *Lemur News* 4: 11–14.

Irwin MT, Samonds KE, Raharison JL, Wright PC (2004). Lemur latrines: observations of latrine behavior in wild primates and possible ecological significance. *Journal of Mammalogy* 85: 420–427.
Irwin MT, Johnson SE, Wright PC (2005). The state of lemur conservation in southeastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx* 39: 204–218.
IUCN (2016). *The IUCN Red List of Threatened Species. Version 2016-1*. http://www.iucnredlist.org (accessed June 30, 2016).
IUCN/SSC (2013). *Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0*. Gland, IUCN Species Survival Commission.
Kelley EA (2013). The ranging behavior of *Lemur catta* in the region of Cap Sainte-Marie, Madagascar. *American Journal of Physical Anthropology* 150: 122–132.
Kelley EA, Sussman RW, Muldoon KM (2007). The status of lemur species and Antserananomby: an update. *Primate Conservation* 11: 71–77.
LaFleur M, Clarke T, Giraud L, Youssouf J, Gould L, Adiba M (2015). Reniala Lemur Rescue Center for ring-tailed lemurs in Madagascar. *Lemur News* 19: 11–13.
Leighty KA, Valuska AJ, Grand AP, Bettinger TL, Mellen JD, Ross SR, Boyle P, Ogden JJ (2015). Impact of visual context on public perceptions of non-human primate performers. *PLoS One* 10: e0118487.
Macdonald DW, Mace GM, Barreto GR (1999). The effects of predators on fragmented prey populations: a case study for the conservation of endangered prey. *Journal of Zoology* 247: 487–506.
Malone M, Ramanamanjato JB, Randriatfika F, Donati G (2013). Habitat structure and grey mouse lemur (*Microcebus murinus*) abundance in the transitional littoral forest of Petriky, south-east Madagascar. *Lemur News* 17: 22–26.
Moniac N, Heitmann A (2007). *Lemur catta* and hunting around Andohahela. *Lemur News* 12: 11.
Naughton-Treves L, Holland MB, Brandon K (2005). The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annual Review of Environment and Resources* 30: 219–252.
Nekaris KAI, Musing L, Vazquez AG, Donati G (2016). Is tickling torture? Assessing welfare towards slow lorises (*Nycticebus* spp.) within web 2.0 videos. *Folia Primatologica* 86: 534–551.
Plumptre AJ, Cox D (2006). Counting primates for conservation: primate surveys in Uganda. *Primates* 47: 65–73.
Pusey A, Pintea L, Wilson ML, Kamenya S, Goodall J (2007). The contribution of long-term research at Gombe National Park to chimpanzee conservation. *Conservation Biology* 21: 623–634.
Rakotoarisoa SV (1999). Contribution à l'étude de l'adaptation de *Lemur catta* Linnaeus, 1758, aux zones sommitales de la Réserve Naturelle d'Andringitra. Mémoire DEA, Université d'Antananarivo.
Razafindramanana J (2011). *Behavioural Ecology of Sympatric Lemur Species* Lemur catta *and* Eulemur *sp. in Forest Fragments, South-Eastern Madagascar.* Doctoral dissertation, Oxford Brookes University.
Reuter KE, Schaefer MS (in press). Motivations for the ownership of captive lemurs in Madagascar. *Anthrozoos*.
Reuter KE, Schaefer MS (2016). Illegal captive lemurs in Madagascar: comparing the use of online and in-person data collection methods. *American Journal of Primatology* DOI: 10.1002/ajp.22541.
Reuter KE, Schaefer MS (2016). Captive conditions of pet lemurs in Madagascar. *Folia Primatologica* 87: 48–63.
Reuter KE, Gilles H, Wills AR, Sewall BJ (2016). Live capture and ownership of pet lemurs in Madagascar: extent and conservation implications. *Oryx* 40: 344–354.
Sauther ML, Sussman RW, Gould L (1999). The socioecology of the ring-tailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8: 102–132.
Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana J, Louis EE Jr, Rajaobelina S (eds.) (2013). *Lemurs of Madagascar: A Strategy for their Conservation 2013–2016.* Bristol, IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International.
Schwitzer C, Mittermeier RA, Johnson SE, Ratsimbazafy J, Razafindramanana J, Louis EE, Chikhi L, Colquhoun IC, Crick J, Dolch R, Donati G, Irwin M, LaFleur M, Nash S, Patel E, Peacock H, Randrianambinina B, Rasolofoharivelo T, Wright P (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science* 343: 842–843.
Siers RS (2007). Research experience in Vohibasia Forest, southwestern Madagaskar. Lemur News 12: 42–43.
Sussman RW, Green GM, Porton I, Andrianasolondraibe OL, Ratsirarson J (2003). A survey of the habitat of *Lemur catta* in southwestern and southern Madagascar. *Primate Conservation* 19: 1631.
Sussman RW, Sweeney S, Green GM, Porton I, Andrianasolondraibe OL, Ratsirarson J (2006). A preliminary estimate of *Lemur catta* population density using satellite imagery. In *Ringtailed Lemur Biology* (Jolly A, Sussman RW, Koyama N, Rasamimanana H, eds.), pp 16–31. New York, Springer.