

Illegal Trade of Wild-Captured *Lemur catta* within Madagascar

Marni LaFleur^a Tara A. Clarke^b Kim E. Reuter^c Melissa S. Schaefer^d
Casey terHorst^e

^aDepartment of Anthropology, University of California San Diego, La Jolla, CA, USA;

^bDepartment of Evolutionary Anthropology, Duke University, Durham, NC, USA;

^cAfrican Field Division, Conservation International, Nairobi, Kenya; ^dDepartment of Anthropology, University of Utah, Salt Lake City, UT, USA; ^eDepartment of Biology, California State University, Northridge, CA, USA

Keywords

Strepsirrhine · Ring-tailed lemur · Pet · Wildlife trafficking · Conservation

Abstract

Lemur catta is the most reported illegal captive lemur. We document 286 *L. catta* that were held in illegal captive conditions in Madagascar. Coastal tourist destinations are “hot spots” for sightings. Many of the *L. catta* reported were in businesses (49%) and were perceived to be held captive for the purpose of generating income (41%). Infant/juvenile *L. catta* were overwhelmingly observed annually in December (41%) and may suffer high mortality rates given that they are not weaned during this month of the year. Population growth modeling suggests that known capture rates may be sustainable in all but small populations of 500 individuals and when infants/juveniles are targeted. However, of the seven remaining populations of *L. catta* with more than 100 individuals, only one is known to contain more than 500 animals, and we present evidence here that infants/juveniles are targeted. Moreover *L. catta* face significant other threats including habitat loss, bushmeat hunting, and climate change. Several actions could reduce the illegal capture and ownership of *L. catta* in Madagascar such as tourist behavior change initiatives, enforcement of laws, and alternative livelihoods for local people. These interventions are urgently needed and could be adapted to protect other exploited wildlife in the future.

© 2019 S. Karger AG, Basel

Introduction

Approximately 60% of all nonhuman primate species are threatened with extinction [Graham et al., 2016; Estrada et al., 2017, 2018]. Primate species decline and local extirpation are attributed to anthropogenic pressures on primates (bushmeat hunting, capture for biomedical experimentation, exotic pet trade) and their habitats (extractive industries and agriculture), along with anthropogenic disease transmission (e.g., Ebola) and climate change [Estrada et al., 2017, 2018; Kalbitzer and Chapman, 2018]. Since human-induced pressures are likely to continue in future, the conservation status of primates remains precarious, although primate experts are hopeful that these trends can be reversed [Estrada et al., 2017, 2018; Chapman et al., 2018].

Although the pet trade has long been recognized as a threat to haplorrhine primates (specifically monkeys and apes) [Soini, 1972; Duarte-Quiroga et al., 2003; Stiles et al., 2013], these threats have only relatively recently been acknowledged for strepsirrhines (lemurs [Reuter et al., 2016], lorises [Nekaris and Jaffe, 2007], and galagos [Svensson et al., 2015]). Slow lorises are among the most commonly traded primates in Indonesian areas [Shepherd et al., 2004; Nijman et al., 2017], with several thousand individuals for sale in certain markets per year [Nijman, 2010]. Moreover, slow lorises gained popularity as pets after a youtube video “Tickling slow loris” went viral in 2009 [Nekaris et al., 2013]; they are now traded across Asia and beyond [Nekaris and Jaffe, 2007; Nekaris et al., 2010]. Additionally, the trade of African lorisiforms (galagos, pottos, angwantibos) appears to be widespread, as a recent online survey reports records from at least 24 African countries [Svensson et al., 2015]. Similarly, within Madagascar, an estimated 28,000 lemurs were kept as illegal pets in urban areas across the island between 2010 and mid-2013 [Reuter et al., 2016].

Lemurs are the most threatened group of mammals on earth, with 94% of lemur species at risk of extinction [Schwitzer et al., 2014]. A variety of direct actions and indirect circumstances have led to most lemur species being threatened with extinction. Direct actions include extensive habitat destruction [Mittermeier et al., 2006], bushmeat hunting [Barrett and Ratsimbazafy, 2009], and the pet trade [Reuter et al., 2016, 2017]. Circumstances contributing to the decline of lemurs include widespread poverty, which leaves millions of people dependent on forest resources for survival [Schwitzer et al., 2014], political instability, corruption, and lack of effective environmental law enforcement [Reuter et al., 2017].

Tourism is an important source of revenue for Madagascar [Schwitzer et al., 2014]. Several national parks, protected areas, and private reserves are within an hour’s drive of Madagascar’s capital city, Antananarivo, which enables thousands of tourists to view lemurs per year [see Mittermeier et al., 2006]. Common tourist activities, such as direct contact with lemurs for photo opportunities, take place in the vicinity of these parks and reserves and may be detrimental to lemur populations [Reuter and Schaefer, 2016a, b; Reuter et al., 2017], as these animals are likely wild-caught. Furthermore, lemurs are often illegally wild-caught in order to supply some resorts and roadside zoos with “added value attractions”, wherein naïve tourists support the practice through direct payment or by patronizing establishments keeping lemurs [Reuter and Schaefer, 2016a, b]. Wild-captured animals are then no longer providing ecosystem services to their native forests (e.g., seed dispersal) or contributing to wild populations through reproduction, both of which are important to species facing extinction. Few entities in Madagascar hold permits to legally keep lemurs

in captivity, and no existing regulations require legal facilities to display permissions to patrons.

The ring-tailed lemur (*Lemur catta*) is Endangered [Andriaholinirina et al., 2014], despite being Madagascar's best known and studied species, and is the most commonly reported lemur in illegal captivity [LaFleur et al., 2015; Reuter and Schaefer, 2016a, b]. Estimates from the years 2016 and 2017 indicate that sharp and continued declines threaten *L. catta* populations [Gould and Sauther, 2016; LaFleur et al., 2017, 2018; but see Murphy et al., 2017]. *L. catta* face many of the same threats as all other lemurs and have suffered localized extirpation for bushmeat hunting [Gardner and Davies, 2014], extraction for the pet trade [Andriaholinirina et al., 2014; LaFleur et al., 2015; Reuter and Schaefer, 2016], and continued and rapid habitat loss particularly in the southernmost dry forests of Madagascar [Brinkmann et al., 2014]. These have taken a significant cumulative toll on abundance and distribution of *L. catta* [Goodman and Raselimanana, 2003; Sussman et al., 2006; Kelley et al., 2007; Gould and Sauther, 2016; LaFleur et al., 2017, 2018; but see Murphy et al., 2017].

We examined interviews and web-based surveys specific to the trade of *L. catta* within Madagascar. We specifically focus on illegal captivity, which excludes facilities such as Tzimbazaza Zoo, Park Ivoloina, Lemurs' Park, and others with express permission to capture and/or keep lemurs within Madagascar. Based on our observations, we made several predictions about the circumstances under which *L. catta* would be found. For example, since pet lemurs are often associated with tourists, we predict that they will be reported more frequently in tourist destinations, associated with businesses catering to tourists, and kept for the purposes of generating income resulting from tourists. Moreover, based on our personal experiences of seeing pet lemurs in Madagascar, we expect that owners of lemurs will be Malagasy. Additionally, because of the costs associated with caring for a pet, we expect that lemur owners will be perceived as wealthy by respondents. We also expect that the trade in *L. catta* has increased over time and use modeling data along with other known threats to assess the sustainability of live extraction of this species. *L. catta* conservation will depend on these data, as the information can aid in determining motivations for capture, ownership, and sale. Subsequently, targeted conservation action can be deployed which addresses root causes of the trade.

Methods

We collected data in two ways, via: (1) in-person interviews and (2) the Pet Lemur Survey (www.petlemur.com), a web-based survey for sightings of pet lemurs [Reuter and Schaefer 2016a, b; Reuter et al., 2016]. We carried out the in-person interviews at households in central, western, and northern Madagascar in 2013, and households in central, eastern, and southern Madagascar in 2016. Both the in-person interviews and web-based surveys broadly asked the same basic questions regarding pet lemurs in Madagascar, and the full methods and data collection protocols are described in Reuter et al. [2016] and Reuter and Schaefer [2016a, b].

By 2016, the combined data set consisted of 1,374 reports of captive lemur sightings, including lemurs from 32 species. Most of these captive lemur sightings were reported by individuals who did not own the lemur. Therefore, some of the information recorded in this database (such as whether or not the owner of the lemur was wealthy) was subjective.

Within the database of 1,374 reports, 232 reports were specific to *L. catta*, though it is clear that some of these reports are of the same captive lemur (despite being reported by different respondents). This risk of "double-counting" of lemurs within the data set was noted in Reuter and

Schaefer [2016b] and in Reuter et al. [2016]. Therefore, we took several steps to identify and eliminate duplicate reports in our data set. This included first removing any reports that did not have the following data with reference to the *L. catta* sighting: year, town, environment (business, residence, other), and method of confinement (cage, tether, etc.). The remaining 180 reports were then carefully analyzed and compared to determine which records likely described unique *L. catta* sightings. We considered the aforementioned variables (year, town, environment, method of confinement), as well as other factors, when applicable. These included the name of the hotel or business, the number of animals observed together, the animals' age (juvenile or adult), and/or the purpose of the pet lemur (personal pet, to make money from tourists, etc.). If we could not ascertain that a report represented a unique animal with reasonable certainty, the account was removed from the data before further analyses were performed. Sample sizes vary between certain aspects of survey information, because respondents could choose to not respond to any question asked.

Of the pet *L. catta* identified we examined the relative numbers of individuals according to the following variables: location, purpose of lemur, nationality and perceived wealth of owner, and trends and sustainability of the trade. We used the χ^2 test to check the goodness of fit of our actual and expected sightings of pet lemurs each month of the year. We further used the F distribution (two-tailed) to analyze variance between the adult and juvenile *L. catta* sightings by environment type (business, residence, other), mechanism of confinement (cage, tether, no cage or tether, other), and the purpose of the lemur (personal pet, to make money, no purpose, other). Respondents were not explicitly asked whether a lemur was a juvenile/infant or an adult; this information was recorded only when it was offered by the respondent ($n = 18$). p values were set to 0.05 in all cases.

We use a stage-structured transition matrix (i.e., Leftkovitch matrix) to determine the effects of capture of *L. catta* females [Bradford and Hobbs, 2008]. There are six biologically meaningful (i.e., those known to affect survival and reproduction) stages in our matrix including: infant/juvenile (under 1 year of age), 1-, 2-, 3-, 4-year-olds, and adults (5–15 years old). In order to understand the effects of population size, we use the hypothetical population sizes of 500, 2,500, 5,000, and 10,000 individual *L. catta*.

We base the number of individuals in each stage on the hypothetical population sizes, stage-specific survivorship and reproduction [Koyama et al., 2001, 2002; Gould et al., 2003], and extracolon rates from the years 2011–2016 (detailed here). The dominant eigenvalue of our matrix represents the population growth rate, λ . Values of λ greater than 1 indicate an increasing population; values less than 1 indicate a decreasing and unsustainable population.

Results

We determined that 180 reports detailing 286 individual *L. catta* were likely unique (Fig. 1). The reports of these animals had unique characteristics that did not match any other reports. To illustrate, they may have been held at a certain named business location with a specified method of confinement, and these characteristics were not found in any other report.

Location and Purpose of Lemurs

Most *L. catta* were observed in Toliara (62, 22%), Anakao (49, 17%), and Fort Dauphin (34, 12%) (Fig. 2). Others were reported in Ambalavao (16, 6%), Antsirabe (3, 1%), Antananarivo (11, 4%), Fianarantsoa (16, 6%), and all other locations throughout the island (95, 33%). Juvenile lemurs were most reported in Anakao (9 out of 17 records of juveniles, 53%) (Fig. 2). Nearly half of the *L. catta* (140, 49%) were viewed in businesses (e.g., hotel resort, restaurant, etc.), while the rest were observed in residences (110, 38%) and other locations (36, 13%), which included “on the

Fig. 1. Overview of Pet Lemur Survey including the numbers of reports and individual *Lemur catta* identified.

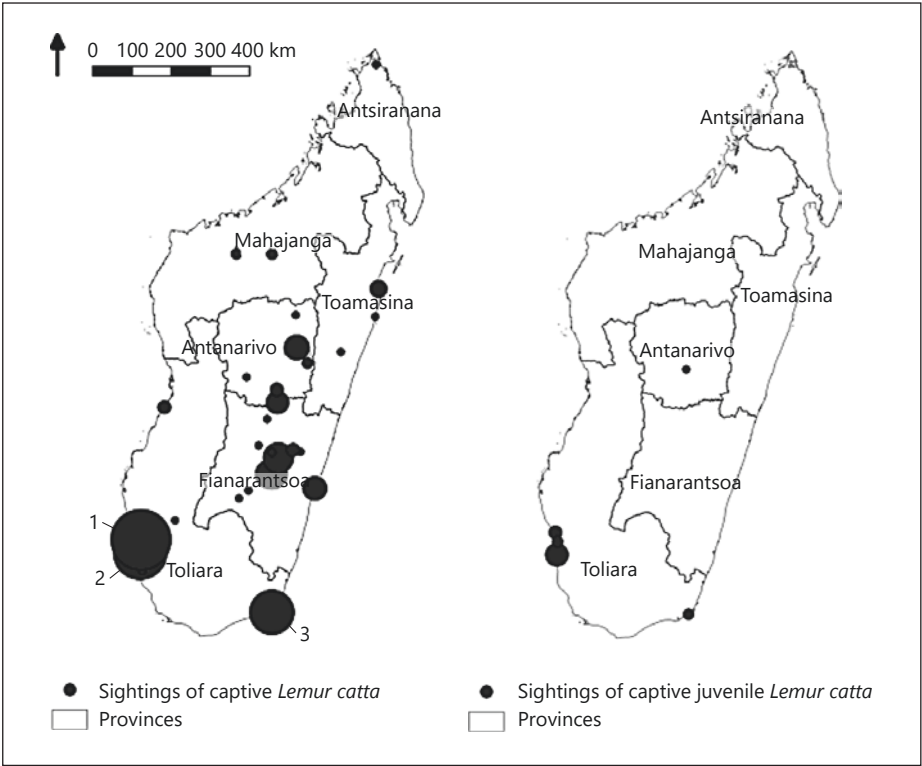
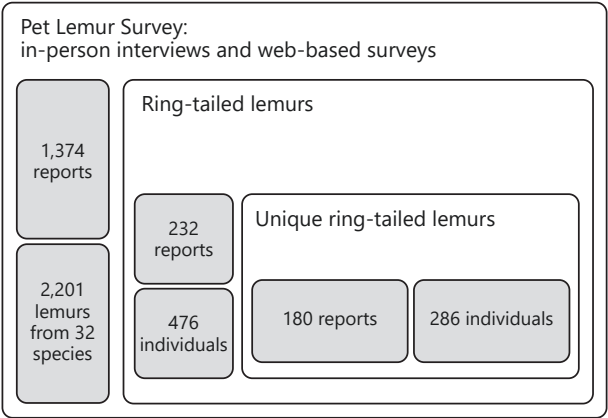


Fig. 2. Maps of Madagascar showing locations of captive *Lemur catta*. Numbers 1–3 indicating the locations with the most lemurs (1, Toliara; 2, Anakao; 3, Fort Dauphin). Dots are sized in proportion to the number of *L. catta* with larger dots indicating more lemurs.

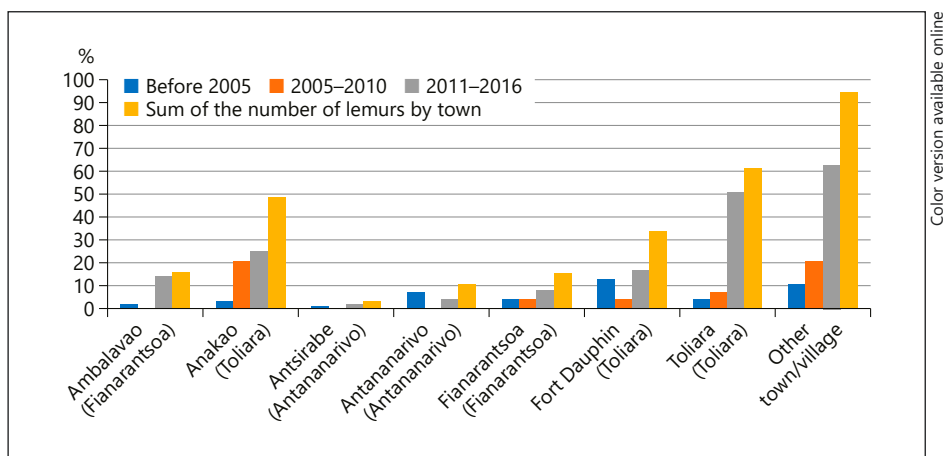


Fig. 3. Location (by town and province) of captive *Lemur catta* reported to the Pet Lemur Survey before 2005, from 2005 to 2010, from 2011 to 2016, and the sum of all reported lemurs regardless of date.

beach”, “on the street”, and simply “other” nonbusiness or residential locations. The purpose for keeping the *L. catta* was reported as income generation (117, 48%, both direct and indirect income generation), as a personal pet (113, 46%), or that it did not serve a purpose (13, 5%). In 15% (37) of responses, the purpose of the lemur was not specified.

Nationality and Perceived Wealth of Lemur Owners

When respondents reported the nationality of the owners (178, 63%), these were most often Malagasy (132, 73%), while some were foreigners (46, 26%), and a small percentage were reported as being both Malagasy and foreigner (2, 1%), for example, when the lemur was owned by a couple in which one individual was Malagasy and the other was a foreigner. In addition, owners of *L. catta* were perceived by respondents as being wealthy (140, 77%), although some were said to have “middle” wealth (5, 4%), and some were not thought of as wealthy (6, 19%).

Trends and Sustainability of Lemur Trade

The year when an *L. catta* was witnessed by a respondent was reported in 286 cases (100%) and *L. catta* sightings were examined. Most *L. catta* were reported from the years 2011–2016 (184, 64%), then 2005–2010 (57, 20%), and finally prior to 2005 (45, 16%) (Fig. 3). The month in which an *L. catta* was spotted was known for 77 of the sightings. The majority of juvenile *L. catta* (7 of 17 records, 41%) were witnessed by respondents in the month of December, while the largest percentage of adults were observed in July (13, 17%) (Fig. 4).

Respondents indicated that many of the pet *L. catta* were still owned or still alive in captivity (49, 43%). Some *L. catta* had been disposed of in some way (27, 34%; escaped, sold, released into the wild), died (14, 17%; natural and intentional deaths), or

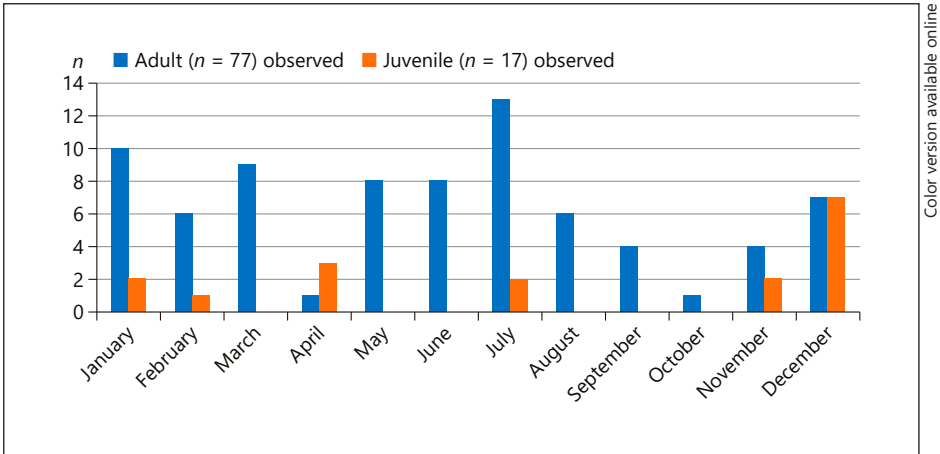
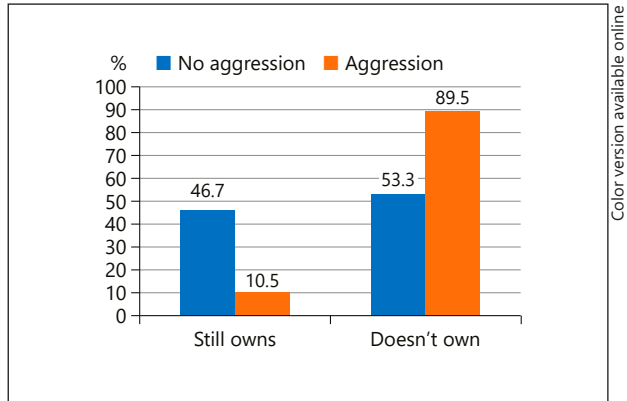


Fig. 4. Month of sighting for adult and juvenile *Lemur catta*.

Fig. 5. Percentage of ring-tailed lemurs that are or are not still cared for by the same owner, according to reported incidences of aggression (still owned by owner, $n = 16$; no longer owned, $n = 33$).



were confiscated by authorities (4, 5%). Individuals with a history of aggression (33, 33%) were less likely to be still owned by the same person (χ^2 test, $df = 1$, p value < 0.001) (Fig. 5).

As expected, larger population sizes have higher population growth rates. Additionally, increased capture rates slow overall population growth. In all but one scenario (with the smallest population, below), populations were still able to grow despite “captures”; however, the growth rate depends on the population size, extraction age class focus, and extraction rate in these instances. Population decline occurred only in the smallest population ($n = 500$) which had 10% extraction that targeted infant/juvenile animals (Table 1).

Table 1. Population growth rates for ring-tailed lemurs for differing population sizes

Ring-tailed lemurs captured per year	λ ($n = 500$)	λ ($n = 2,500$)	λ ($n = 5,000$)	λ ($n = 10,000$)
None	1.24	1.69	1.93	2.22
1.5% of population	1.23	1.66	1.90	2.19
10% of population (any age class)	1.12	1.52	1.74	2.00
10% of population (adult age class only)	1.18	1.60	1.83	2.12
10% of population (infant/juvenile age class only)	0.83*	1.11	1.26	1.43

$n = 500, 2,500, 5,000$, and $10,000$ and scenarios with capture rates ranging from none to 10% of known remaining populations, per year, noting differences in adult and infant/juvenile age classes at 10% extraction. *Indicates population decline.

Discussion

Our database documents 286 different *L. catta* in captivity in Madagascar of which 184 unique individuals were reported between 2011 and 2016. In addition, our database includes 18 juvenile animals (17 are included in analyses, as one of the juveniles did not have a location within the report), some of which undoubtedly died shortly after being observed by Pet Lemur Survey respondents (see below). Our database does not include an exhaustive list of all *L. catta* kept in illegal captivity in Madagascar and is therefore an underestimation of the total number of *L. catta* that have been extracted from the wild for the pet trade in recent years.

Hot spots for pet *L. catta* included Toliara, Anakao, and Fort Dauphin. Each of these locations are popular tourist destinations within the natural range of *L. catta* [Goodman et al., 2006]. Illegal trafficking of primates for the purposes of tourist interactions have been documented with slender lorises (*Loris* spp.) in India [Kanagavel et al., 2013], tarsiers (*Carlito syrichta*) in the Philippines [Yang-Martinez, 2011], barbary macaques (*Macaca sylvanus*) in Morocco [Bergin and Nijman, 2014], and white-handed gibbons (*Hylobates lar*) in Thailand [Grey, 2012; Osterberg et al., 2015]. In these locales, tourists often seek encounters with wildlife, including primates, so that they can take photographs for sharing via social networks [Osterberg and Nekaris, 2015]. Using primates as photo props for tourists has presented threats to primates in the past [Clark, 1997] but may be increasing in popularity and can be lucrative for primate traffickers [Goodman, 1993; Svensson and Friant, 2014; Osterberg and Nekaris, 2015; Nijman and Healy, 2016].

In our study, we found that half (49%) of the *L. catta* reported in our database were observed in businesses (e.g., hotels, restaurants) and were perceived to serve the purpose of generating income. In comparison, when all lemur species were aggregated together, they were kept for money-making purposes just 20% of the time [Reuter and Schaefer, 2017]. It may be that *L. catta* are used for money-making purposes more often than other lemur species because they are well known and easily recognizable. *L. catta* are commonly kept in zoos globally and are an iconic species in Madagascar and are often used on billboards and other advertisements targeting

tourists [M.L., pers. observation]. Recognition of this charismatic species likely makes them attractive to tourists and, in turn, local entrepreneurs.

Captive *L. catta* can be a source of both direct and indirect income. For example, patrons (including foreign tourists) may pay directly to interact with the animal (sometimes with the promise of photo opportunities) [LaFleur et al., 2015] or may simply patronize businesses, such as restaurants, that keep captive *L. catta* [Goodman, 1993; Reuter and Schaefer, 2016a, b]. People who own *L. catta* charge between 30 cents and 3 USD for photos or a chance for an up-close interaction [LaFleur et al., 2015]. Keeping illegal captive lemurs can be especially profitable for hotels; hotels in Madagascar that advertised having captive lemurs on their websites or social media pages, charged an average of USD 25.69 more per night than those that did not [Reuter and Schaefer, 2016b].

In addition to income generation or business promotion, *L. catta* are also kept as personal pets. Nonhuman primates are kept as pets globally, for a variety of reasons including for religious beliefs [see Nijman and Healy, 2016], as a symbol of wealth and status [Svensson and Friant, 2014], or because they are considered companions or are generally pleasing to be around [Duarte-Quiroga and Estrada, 2003; Reuter and Schaefer, 2017]. Most of the *L. catta* owners identified here were Malagasy and were perceived as being relatively wealthy. This suggests that having lemurs may demonstrate wealth or social status, as was indicated by some respondents of Pet Lemur Survey. It may also indicate that people without relative wealth may not be able to keep captive lemurs, given the expenses associated with keeping and feeding these animals.

L. catta having a history of aggression were far less likely to continue to be owned by the same person. Aggressive and other abnormal behaviors are common in wild-caught captive *L. catta*, particularly after the animals reach sexual maturity (3–4 years of age) [LaFleur et al., 2015]. These aggressive animals often become a nuisance to their owners and the owners' neighbors, as they may bite or lunge at those living in close proximity [LaFleur et al., 2015]. Aggressive lemurs may be given away, released, caged, abused, or even killed for their perceived bad behavior. Anecdotally we have been told of *L. catta* having tails or fingers amputated, or bones intentionally broken, as a result of aggressive behavior, and have also observed rescued *L. catta* with indications of amputations/abuse. Physical repercussions by owners for biting humans or aggressiveness towards humans have also been noted for wild-caught capuchins (*Cebus apella margaritae*) in Venezuela [Ceballos-Mago and Chivers, 2010], and wild-caught spider and howler monkeys (*Ateles geoffroyi*, *Alouatta pigra*, and *A. palliata*) in Mexico [Duarte-Quiroga and Estrada, 2003].

Restricted annual reproduction in *L. catta* results in births during late September and early October of each year, while weaning generally takes place in February and March [Sautther et al., 1999] but can be as late as May [M.L., pers. observation]. Juvenile captive *L. catta* were (42% of 17 sightings) witnessed in the month of December. This could be because (1) infants being targeted for extraction at or before the peak of the tourist season in December, (2) more respondents are viewing and reporting the infants during this high season for tourism. Anecdotal reports indicate that when cruise ships dock in Anakao, men from the village make day trips to forested areas, such as Tsimanampesotse National Park, to collect infant *L. catta*. This suggests that infants are specifically targeted but should be investigated further to disentangle the effect of increased respondent presence. Captured infants may be unlikely to survive

because they are dependent upon their mothers for milk until at least the month of February. In fact, several respondents noted poor condition of the juvenile lemurs and used the following words to describe the juvenile lemur's condition: "dehydrated", "dirty", "floppy", and "near death". Although we expect increased mortality in wild-captured infants who are not yet weaned, this will be important to explore in future, as we do not currently have evidence to support this claim directly. Targeted infant extractions can have negative implications for threatened species, as they can disrupt the normally occurring age and sex structures of populations and thus impede population growth or maintenance [Ceballos-Mago and Chivers, 2010].

Our transition matrix data suggest that extraction of up to 10% of *L. catta* populations (with 500, 2,500, 5,000, and 10,000 individuals) per year will still allow for positive population growth. Population growth is significantly curtailed when infants/juveniles are targeted and becomes negative in the case of the smallest population ($n = 500$). Results obtained with transition matrix data report that the extraction rates documented here (i.e., 184 individuals between 2011 and 2016) are not likely to impact remaining *L. catta*; however, there are a number of additional factors that must be considered that are likely to falsify these interpretations. First, although there are thought to be several thousand *L. catta* remaining in the wild, populations are patchily distributed and isolated from one another [Gould and Sauther, 2016; LaFleur et al., 2017, 2018; Murphy et al., 2017]. In fact, we only know of seven locations where there are more than 100 individuals, and one location where there are more than 500 individuals (LaFleur et al., 2018). Thus, if animals are being taken from populations with 500 or fewer individuals remaining (which the vast majority likely are), and infants/juveniles are targeted (which we have presented evidence for here), even extraction of 10% will prohibit population growth in each of the populations. Second, extraction rates are likely higher than what we have documented, simply because our sample effort is insufficient and also because captured infant lemurs may die within the first week following capture [see Reuter et al., 2016] and are thus not likely to be observed (and subsequently reported, for the purposes of this study). Third, live capture for the pet trade is not the only threat that *L. catta* are facing. *L. catta* populations have experienced dramatic declines in the last three decades [Goodman and Raselimanana, 2003; Sussman et al., 2006; Kelley et al., 2007; Gould and Sauther, 2016; LaFleur et al., 2017, 2018; but see Murphy et al., 2017], resulting from habitat degradation and destruction [Brinkmann et al., 2014], bushmeat hunting [e.g., Sussman et al., 2006], and live capture for the pet trade [LaFleur et al., 2015; LaFleur et al., 2017, 2018]. The combination of small isolated remaining populations along with existing threats *L. catta* is facing may simply be more than they can persist under, despite being a resilient species.

What Can Be Done?

Educating Tourists and Promoting Primate-Friendly Tourism

Many tourists who visit Madagascar seek up-close experiences with lemurs, yet few are aware of the negative impacts that their actions may have on wildlife [Moorhouse et al., 2015]. Tourists, who may have little knowledge of the conservation status of nondomestic animals, often rely on the information provided by destination guides or staff assuming that regulating bodies oversee wildlife interactions [Moorhouse et al., 2017]. Destination guides and/or staff may not have correct information or might be willing to share information that they believe tourists want to hear, and regulating

bodies may not be in place or effective at protecting wildlife. Moreover, *L. catta* and other iconic animals that are prevalent in media are less likely to be thought of as threatened by extinction [Leighty et al., 2015; Courchamp et al., 2018]. This combination of factors wherein tourists are motivated to seek close encounters with wildlife, yet have little information on the negative effects their interactions may have, can significantly impact the conservation of certain species, such as *L. catta*.

Given the apparent link between *L. catta* extraction from the wild and tourism, it is important to decrease the tourist demand to interact with wildlife in nonnatural environments [Sablich, 2016]. Steps have already been taken at the international scale; for example, TripAdvisor [2018] – a popular travel-booking service – announced in October 2016 that it would stop selling tickets for wild animal attractions involving endangered species [Sablich, 2016]. At the national scale, no outreach campaigns have targeted foreign and/or domestic tourists, other than our recent pilot project entitled “keeping lemurs wild”. Tourist education and awareness initiatives are imperative for decreasing demand for direct human-lemur interactions, and therefore indirectly decreasing the illegal capture of lemurs from the wild. Ideally, outreach campaigns would ensure that tourists cease to patronize establishments that are exploiting lemurs and stop paying to interact or take photographs of/with illegally held captive lemurs. Moving forward, information on ethical interactions with lemurs should be made widely available, even before a tourist arrives in Madagascar (e.g., via guidebooks, on websites such as TripAdvisor, on in-flight magazines). Posters and leaflets would also be useful at large international entry points (such as airports), from the Madagascar Office of Tourism, and through tourist-centric print and digital media.

Educating Locals, Mobilizing Law Enforcement, and Caring for Confiscated Lemurs

Many people in Madagascar seem to be aware that having a captive lemur is illegal [Reuter et al., 2016] but enforcement of the law is low; this is notable given that three quarters of the owners of *L. catta* were Malagasy. Knowledge alone is not a sufficient deterrent to harboring illegal lemurs and neither are the current enforcement mechanisms, which are unlikely to be changed in the coming years (national enforcement of lemur hunting bans is considered unlikely) [Sommerville et al., 2010]. Malagasy people generally believe that lemurs are plentiful and not threatened by extinction, despite the fact that policymakers at national and international levels believe lemurs to be under extreme danger of extinction [Gore et al., 2016]. This low perceived threat by local people is a barrier to effective management, and important to address in communications, outreach, and/or education activities [Britt et al., 2004]. Decreasing extraction of wild caught lemurs in this context requires a multi-pronged approach that includes: (1) general outreach to the public; (2) outreach and capacity building within government and enforcement agencies; and (3) increased enforcement and prioritization of this issue by the government (including not just enforcement of the law, which can include fines, jail time, and confiscation of the lemur, but also planning for lemur well-being after confiscation).

Although increased enforcement is necessary to reduce the illegal trade of wild lemurs, very few legal captive facilities in Madagascar are capable of hosting confiscated lemurs and, to our knowledge, none of these entities has successfully released *L. catta* back into the wild. This may be because captive lemurs (who were likely cap-

tured at a young age) are not likely to possess the skills necessary for wild survival [Britt et al., 2004] and because reintroduction into the wild requires significant investment of resources. Moreover, since only a few captive facilities in Madagascar care for confiscated or abandoned captive lemurs (ONG Reniala Lemur Rescue Center; Reniala at SIB Mahajanga), a large number of newly confiscated animals could not realistically be accommodated by existing facilities. Therefore, while reintroduction of rehabilitated captive lemurs (i.e., those that have acquired the skills necessary for wild survival) could be a viable solution for some confiscated animals, this is a long and expensive process that will likely have only limited success. Efforts should be concentrated on preventing further wild capture, given the complications and difficulties associated with rehabilitation and reintroduction of former pets.

Alternative Means of Income Generation

Madagascar is plagued with extreme poverty, particularly in the southwestern regions of the country, where drought and famine are common. Alternative and sustainable mechanisms of income generation may be a viable means of offsetting lost opportunities to individuals who would otherwise capture or purchase *L. catta* for the purpose of earning money. In Zambia, individuals specifically responsible for high levels of natural resource depletion were trained in alternative income generation (food production and sale), which led to increased biodiversity conservation [Lewis et al., 2011]. Possible alternatives could include training in the production of sustainable handcrafts, specifically those with a low skill entry point and that require little upfront investment. The production and sale of beaded craft items by Maasai have been effective in conserving wildlife in Kenya [van Vliet, 2011].

For businesses that keep lemurs, a different strategy is required, since owners are not likely to be motivated by earning relatively small amounts of money. One potential solution that has been proposed by Lemur Love, an NGO working in Madagascar (M.L. is affiliated with this NGO), is a “Lemur Alliance” whereby businesses voluntarily pledge to not keep illegal lemurs, in exchange for listings in “lemur-friendly” business directories. As tourists become more aware, they could seek out and primarily patronize businesses that are listed, thus giving the businesses a competitive advantage through their Lemur Alliance membership. TripAdvisor has implemented a program to help potential patrons identify eco-friendly hotels [TripAdvisor: Green Leaders, 2018]. To our knowledge no such program exists to help tourists identify businesses that protect wildlife, but this has the potential to be a significant motivator for certain clientele.

Conclusions

Primates face many anthropogenic threats to their survival. Strepsirrhines are wild-captured and kept in captive environments. Wild capture both for income generation and personal ownership poses threats to many lemur species, and particularly *L. catta*, which are the most frequently reported pet lemur. *L. catta* have experienced dramatic declines in their range and population numbers and extirpations in the wild [Goodman and Raselimanana, 2003; Sussman et al., 2006; Kelley et al., 2007; Gould and Sauther, 2016; LaFleur et al., 2017, 2018; but see Murphy et al., 2017], animals may suffer low survivorship after capture (although this should be confirmed

with future research) [LaFleur et al., 2015], and among those surviving, many have poor-quality lives and may not be suitable for wild release [Reuter and Schaefer, 2016b]. Conservation actions focused on tourist education, enforcement of Malagasy law, and development of alternative economic livelihoods at the individual and business levels are promising directions for reducing the illegal capture and trafficking of lemurs. These interventions are urgently needed and could be adapted to protect other exploited wildlife in the future.

Acknowledgments

We first thank all of the individuals who voluntarily provided information for this study. 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. Many thanks to GERP (Groupe d'étude et de recherche sur les primates de Madagascar), Association Mitsinjo, the Sainte Luce Reserve, and to Conservation International for facilitating research in some of the towns visited in 2016 survey efforts. We also wish to thank Lydia Greene and Holly Schneider-Brown for their dedication to forwarding lemur conservation and awareness, and Toby Schaeffer for the production of maps for this manuscript. Additionally, we thank Anna Nekaris (academic editor), and anonymous reviewers for their feedback, which significantly improved this paper.

Statement of Ethics

We followed international standards of research ethics, and research protocols were reviewed and approved by an ethics oversight committee (University of Utah Institutional Review Board). All researchers completed ethics training through the Collaborative Institutional Training Initiative. This research did not involve work on animals. All laws relevant to the survey of adult populations were followed.

Disclosure Statement

The authors have no conflicts of interest to declare.

Funding Sources

Funding for this project was generously provided by the Margo Marsh Biodiversity Foundation (ML 2016–2017, TAC 2017–2018) and the National Geographic Society (KER C313-15).

Author Contributions

Author contributions are as follows: conception (K.E.R.); data collection, analyses, and interpretation (all authors), drafting manuscript (M.L.), critical revision and final approval (all authors).

References

- Andriaholinirina N, Baden A, Blanco M, Chikhi L, Cooke A, Davies N, et al. (2014). *Lemur catta*. The IUCN Red List of Threatened Species. Version 2014.2. <http://www.iucnredlist.org>.
- Barrett MA, Ratsimbazafy J (2009). Luxury bushmeat trade threatens lemur conservation. *Nature* 461: 470.
- Bergin D, Nijman V (2014). Illegal and open wildlife trade in Morocco's capital. *Swara* July-September: 54–57.
- Bradford JB, Hobbs NT (2008). Regulating overabundant ungulate populations: an example for elk in Rocky Mountain National Park, Colorado. *Journal of Environmental Management* 86: 520–528.
- 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.
- Britt A, Welch C, Katz A, Iambana B, Porton I, Junge R, Crawford G, Williams C, Haring D (2004). The re-stocking of captive-bred ruffed lemurs (*Varecia variegata variegata*) into the Betampona Reserve, Madagascar: methodology and recommendations. *Biodiversity and Conservation* 13: 635–657.
- Ceballos-Mago N, Chivers DJ (2010). Local knowledge and perceptions of pet primates and wild Margarita capuchins on Isla de Margarita and Isla de Coche in Venezuela. *Endangered Species Research* 13: 63–72.
- Chapman CA, Omeja PA, Kalbitzer U, Fan P, Lawes MJ (2018). Restoration provides hope for faunal recovery: changes in primate abundance over 45 years in Kibale National Park, Uganda. *Tropical Conservation Science* 11: 1940082918787376.
- Clark M (1997). The mongoose lemur *Eulemur mongoz* on Anjouan, Comores. *Dodo* 33: 36–44.
- Courchamp F, Jaric I, Albert C, Meinard Y, Ripple WJ, Chapron G (2018). The paradoxical extinction of the most charismatic animals. *PLoS Biology* 16: e2003997.
- Duarte-Quiroga A, Estrada A (2003). Primates as pets in Mexico City: an assessment of the species involved, source of origin, and general aspects of treatment. *American Journal of Primatology* 61: 53–60.
- Estrada A, Garber PA, Mittermeier RA, Wich S, Gouveia S, Dobrovolski R, Nekaris KAI, Nijman V, Rylands AB, Maisels F, Williamson EA (2018). Primates in peril: the significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation. *Peer Journal* 6: e4869.
- Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, et al. (2017). Impending extinction crisis of the world's primates: why primates matter. *Science Advances* 1: e1600946.
- Gardner CJ, Davies ZG (2014). Rural bushmeat consumption within multiple-use protected areas: qualitative evidence from southwest Madagascar. *Human Ecology* 42: 21–34.
- Goodman SM (1993). A reconnaissance of Ile Sainte Marie, Madagascar: the status of the forest, avifauna, lemurs and fruit bats. *Biological Conservation* 65: 205–212.
- Goodman SM, Raselimanana A (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 US.
- Gore ML, Lute ML, Ratsimbazafy JH, Rajaonson A (2016). Local perspectives on environmental insecurity and its influence on illegal biodiversity exploitation. *PloS One* 11: e0150337.
- Gould L, Sauther ML (2016). Going, going, gone... Is the iconic ring-tailed lemur (*Lemur catta*) headed for imminent extirpation. *Primate Conservation* 30: 89–101.
- Gould L, Sussman RW, Sauther ML (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. *American Journal of Physical Anthropology* 120: 182–194.
- Graham TL, Matthews HD, Turner SE (2016). A global-scale evaluation of primate exposure and vulnerability to climate change. *International Journal of Primatology* 37: 158–174.
- Grey S (2012). Conservation difficulties for *Hylobates lar*: white-handed gibbons and Thailand's illegal pet trade. *Consortium: A Journal of Crossdisciplinary Inquiry* 2012: 45–59.
- Kalbitzer U, Chapman CA (2018). Primate responses to changing environments in the Anthropocene. In *Primate Life Histories, Sex Roles, and Adaptability* (Kalbitzer U, Jack KM, eds.), pp 283–310. Cham, Springer.
- Kanagavel A, Sinclair C, Sekar R, Raghavan R (2013). CEPF Western Ghats special series: moolah, misfortune or spinsterhood? The plight of slender loris *Loris lydekkerianus* in southern India. *Journal of Threatened Taxa* 5: 3585–3588.
- Kelley EA, Sussman RW, Muldoon KM (2007). The status of lemur species at Antserananomby: an update. *Primate Conservation* 11:71–77.

- Koyama N, Nakamichi M, Ichino S, Takahata Y (2002). Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989–1999. *Primates* 43: 291–314.
- Koyama N, Nakamichi M, Oda R, Miyamoto N, Ichino S, Takahata Y (2001). A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates* 42: 1–4.
- 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.
- LaFleur M, Clarke TA, Reuter K, Schaeffer T (2017). Rapid decrease in populations of wild ring-tailed lemurs (*Lemur catta*) in Madagascar. *Folia Primatologica* 87: 320–330.
- LaFleur M, Gould L, Sauther M, Clarke T, Reuter K (2018). Re-stating the case for sharp population decline in *Lemur catta*. *Folia Primatologica* 89: 295–304.
- 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.
- Lewis D, Bell SD, Fay J, Bothi KL, Gatere L, Kabila M, Mukamba M, Matokwani E, Mushimbalume M, Moraru CI, Lehmann J (2011). Community Markets for Conservation (COMACO) links biodiversity conservation with sustainable improvements in livelihoods and food production. *Proceedings of the National Academy of Sciences of the United States of America* 108: 13957–13962.
- Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, Ratsimbazafy J, et al. (2006). *Lemurs of Madagascar: Conservation International Tropical Field Guide Series*. Washington, Conservation International.
- Moore RS, Wihermanto S, Nekaris KAI (2014). Compassionate conservation, rehabilitation and translocation of Indonesian slow lorises. *Endangered Species Research* 26: 93–102.
- Moorhouse TP, Dahlsjö CA, Baker SE, D’Cruze NC, Macdonald DW (2015). The customer isn’t always right – conservation and animal welfare implications of the increasing demand for wildlife tourism. *PloS One* 10: e0138939.
- Moorhouse T, D’Cruze NC, Macdonald DW (2017). Unethical use of wildlife in tourism: what’s the problem, who is responsible, and what can be done? *Journal of Sustainable Tourism* 25: 505–516.
- Murphy AJ, Ferguson B, Gardner CJ (2017). Recent estimates of ring-tailed lemur (*Lemur catta*) population declines are methodologically flawed and misleading. *International Journal of Primatology* 38: 623–628.
- Nekaris KAI, Jaffe S (2007). Unexpected diversity of slow lorises (*Nycticebus* spp.) within the Javan pet trade: implications for slow loris taxonomy. *Contributions to Zoology* 76: 187–196.
- Nekaris KAI, Campbell N, Coggins TG, Rode EJ, Nijman V (2013). Tickled to death: analysing public perceptions of “cute” videos of threatened species (slow lorises – *Nycticebus* spp.) on Web 2.0 Sites. *PloS One* 24: e69215.
- Nekaris KAI, Shepherd CR, Starr CR, Nijman V (2010). Exploring cultural drivers for wildlife trade via an ethnoprimateological approach: a case study of slender and slow lorises (*Loris* and *Nycticebus*) in South and Southeast Asia. *American Journal of Primatology* 72: 877–886.
- Nijman V (2010). An overview of international wildlife trade from Southeast Asia. *Biodiversity and Conservation* 19: 1101–1114.
- Nijman V, Healy A (2016). Present-day international primate trade in historical context. In *An Introduction to Primate Conservation* (Wich SA, Marshall AJ, eds.), pp 129–142. Oxford, Oxford University Press.
- Nijman V, Spaan D, Rode-Margono EJ, Nekaris KAI (2017). Changes in the primate trade in Indonesian wildlife markets over a 25-year period: fewer apes and langurs, more macaques, and slow lorises. *American Journal of Primatology* 79: e22517.
- Osterberg P, Nekaris KAI (2015). Conservation implications of the use of photo prop animals for tourism in Thailand: a slow loris case study (*Nycticebus* spp.). *TRAFFIC Bulletin* 27: 13–18.
- Osterberg P, Samphanthamit P, Maprang O, Punnadee S, Brockelman WY (2015). Gibbon (*Hylobates lar*) reintroduction success in Phuket, Thailand, and its conservation benefits. *American Journal of Primatology* 77: 492–501.
- Reuter KE, Schaefer MS (2016a). Illegal captive lemurs in Madagascar: comparing the use of online and in-person data collection methods. *American Journal of Primatology* 79: 1–9.
- Reuter KE, Schaefer MS (2016b). Captive conditions of pet lemurs in Madagascar. *Folia Primatologica* 87: 48–63.
- Reuter KE, Schaefer MS (2017). Motivations for the ownership of captive lemurs in Madagascar. *Anthrozoö* 30: 33–46.
- Reuter KE, Gilles H, Wills AR, Sewall BJ (2016). Live capture and ownership of lemurs in Madagascar: extent and conservation implications. *Oryx* 50: 344–354.
- Reuter KE, LaFleur M, Clarke TA (2017). Endangered species: illegal lemur trade grows in Madagascar. *Nature* 541: 157.
- Sablich J (2016). TripAdvisor to stop selling tickets to many animal attractions. The New York Times. <http://www.nytimes.com/2016/10/11/travel/tripadvisor-to-stop-selling-tickets-to-many-animal-attractions.html>.

- Sauther ML, Sussman RW, Gould L (1999). The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8: 120–132.
- Schwitzer C, Mittermeier RA, Johnson SE, Donati G, Irwin M, Peacock H, et al. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science* 343: 842–843.
- Shepherd CR, Sukumaran J, Wich SA (2004). Open Season: An Analysis of the Pet Trade in Medan, Sumatra 1997–2001. Petaling Jaya, TRAFFIC Southeast Asia.
- Soini P (1972). The capture and commerce of live monkeys in the Amazonian region of Peru. *International Zoo Yearbook* 12: 26–36.
- Sommerville M, Milner-Gulland EJ, Rahajaharison M, Jones JP (2010). Impact of a community-based payment for environmental services intervention on forest use in Menabe, Madagascar. *Conservation Biology* 24: 1488–1498.
- Stiles D, Redmond I, Cress D, Nellemann C, Formo RK (eds) (2013). Stolen Apes – The Illicit Trade in Chimpanzees, Gorillas, Bonobos and Orangutans. A Rapid Response Assessment. United Nations Environment Programme, GRID-Arendal. https://www.occrp.org/images/stories/food/RRAapes_screen.pdf if you want to check ref. format.
- 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 6–31. New York, Springer US.
- Svensson MS, Friant SC (2014). Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia. *Endangered Species Research* 23: 107–114.
- Svensson MS, Ingram DJ, Nekaris KAI, Nijman V (2015). Trade and ethnozoological use of African lorisiforms in the last 20 years. *Hystrix* 26: 153–161.
- TripAdvisor: Green Leaders (2018). <https://www.tripadvisor.com/GreenLeaders>.
- van Vliet N (2011). Livelihood Alternatives for the Unsustainable Use of Bushmeat. Report prepared for the CBD Bushmeat Liaison Group. Technical Series No. 60, Montreal, Secretariat of the Convention on Biological Diversity. <https://www.cbd.int/doc/publications/cbd-ts-60-en.pdf>.
- Yang-Martinez S (2011). *An Investigation of Tarsier Tourism in Bohol, Philippines: Assessments of 11 Tarsier Exhibits, a Worry for Tarsier Welfare and Conservation*. MSc thesis, Oxford Brookes University, Oxford.