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Front cover: Andy Sabin's dwarf lemur, *Cheirogaleus andysabini*, a new species discovered in the Montagne d'Ambre National Park, Antsiranana Province, Madagascar, and described here by Runha Lei and colleagues (see pages 43–54). Photograph by Edward E. Louis, Jr., Omaha's Henry Doorly Zoo and Aquarium.

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Contents

General

The Conservation Impact of the American Society of Primatologists' Conservation Small Grant Program
Neotropics
The Distribution and Taxonomy of Titi Monkeys (Callicebus) in Central and Southern Peru, with the Description of a New Species
Current Status and Threats to <i>Lagothrix flavicauda a</i> nd Other Primates in Montane Forest of the Región Huánuco31 Rolando Aquino, Ricardo Zárate, Luís López, Gabriel García and Elvis Charpentier
Madagascar
A New Species in the Genus <i>Cheirogaleus</i> (Cheirogaleidae)
Home Range Size and Social Organization of the Sahamalaza Sportive Lemur, <i>Lepilemur sahamalazensis</i>
Ring-tailed Lemurs (<i>Lemur catta</i>), Forest Fragments, and Community-level Conservation in South-central Madagascar 67 Lisa Gould and P. Andrianomena
Expanding Knowledge on Life History Traits and Infant Development in the Greater Bamboo Lemur (<i>Prolemur simus</i>): Contributions from Kianjavato, Madagascar
Africa
Assessing the Population Status of the Critically Endangered Niger Delta Red Colobus (<i>Piliocolobus epieni</i>)
Habitat Use by Geoffroy's White-thighed Colobus in the Kikélé Sacred Forest: Activity Budget, Feeding Ecology and Selection of Sleeping Trees
Distribution and Conservation Status of the Mount Kilimanjaro Guereza <i>Colobus guereza caudatus</i> Thomas, 1885107 Thomas M. Butynski and Yvonne A. de Jong
Geza Teleki and the Emergence of Sierra Leone's Wildlife Conservation Movement
Asia
Primates as Flagships for Conserving Biodiversity and Parks in Indonesia: Lessons Learned from West Java and North Sumatra

The Conservation Impact of the American Society of Primatologists' Conservation Small Grant Program

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Abstract: Given the dire condition of existing biodiversity and the limited availability of funding to protect it, conservation practitioners and scholars are increasingly recognizing the need to monitor and evaluate conservation investments. In line with this trend, our objective was to assess the conservation impact of the American Society of Primatologists' (ASP) Conservation Small Grant Program. Since 1989, the ASP has provided funding in support of research- and education-based projects aimed at effecting primate conservation. To date, 185 projects on 74 primate species have been supported in 41 countries. To accomplish our objective, we developed and administered a voluntary survey to former grant recipients from the years of 1997–2012 to assess whether ASP funded projects resulted in further research, dissemination of results, capacity building and other conservation outcomes. We also assessed grant recipients' perceptions regarding factors that impeded conservation outcomes and factors that would have facilitated greater success. Of the 106 people we contacted, 42 responded, giving a 39.6% response rate. Seventy-nine percent of respondents reported at least one conservation outcome. The two most frequently reported outcomes were: (1) research presence generates greater local awareness/interest in target species and/or its habitat, and (2) increased scientific understanding of target species. None of the respondents reported outcomes directly related to the status of the target primate species. Capacity building through the training and employment of students, local people, and protected area staff was reported by 81% of respondents. Almost all of the respondents (93%) disseminated their project results in some fashion (e.g., scholarly journals, newspapers, local radio and TV, conference presentations, and presentations to local schools and communities). The top five factors impeding conservation outcomes were: (1) limited funding, (2) limited time, (3) illegal resource extraction, (4) changes in local government, and (5) lack of support from local people. The top three suggestions for ensuring more successful outcomes were: (1) develop partnerships with local governments and NGOs, (2) establish a long-term research presence, and (3) secure follow-up funding. Overall, the results highlight the importance of garnering local support for primate conservation projects, sustaining a long-term research presence at field sites, clearly defining terms used in monitoring and evaluation, building evaluation into the design of primate conservation projects, and encouraging and enabling researchers to share both successes and failures.

Key Words: ASP, capacity building, conservation evaluation, funding, primate conservation, success

Introduction

Despite an expanded interest in the preservation and protection of global biodiversity, resources available for conservation remain inadequate (James *et al.* 1999; McCarthy *et al.* 2012). To ensure effective use of those limited resources, it is therefore critical that focus be directed toward evaluating the success of conservation initiatives. Accordingly, in the past few decades there has been an increase in the development and use of tools to monitor and evaluate investments in biodiversity conservation (Sutherland *et al.* 2004; Ferraro and Pattanayak 2006). In an "age of accountability," donors, aid

agencies, and international non-governmental organizations are demanding greater transparency and disclosure of results (Christensen 2003). Evaluation requires a clear understanding of what constitutes "success," which can vary widely depending on people's values and the contexts in which the initiatives are conducted. For example, conservation activities can be both direct (for example, species management) and indirect (for example, capacity-building and conservation education) (Kapos *et al.* 2008), but are both types of action on equal footing with regard to what counts as successful? In order to better measure success, scholars have called for a shift in emphasis on "inputs" (for example, monetary investment)

1

and "outputs" (for example, conservation brochures) to the reporting of "outcomes" (for example, increased population size of targeted species) (Ferraro and Pattanyak 2006; Kapos *et al.* 2008; Bottrill *et al.* 2011).

In line with these trends in conservation evaluation, our objective was to conduct an assessment of the conservation impact of the American Society of Primatologists (ASP) Conservation Small Grant Program. This fund is one of a handful of programs that provide small grants (i.e., less than \$5000) for projects aimed at the protection and conservation of nonhuman primate populations. According to the IUCN (2015), 54% of the 633 primate taxa are currently threatened with extinction, and the percentage continues to increase each year. Primates across the world are threatened primarily by human activities, with more than half experiencing habitat degradation or loss, and hunting or live capture (Oates 2013). These conditions can lead to rapidly declining populations, making primate conservation an urgent concern. For many, primates are considered intrinsically important and worthy of the conservation efforts aimed at protecting them. Primates also have ecological and cultural value to humans (Riley et al. 2011). For example, forest health may depend on primates as seed dispersers, thereby ensuring the regeneration of the ecological systems in which they live (Chapman 1995; Lambert and Garber 1998). In addition, primates can be valuable to a nation's sense of pride, a local tourism-based economy, or a religious worldview (Wheatley 1999; Hill 2002; McKinney 2014).

Since the ASP, a scholarly and educational society dedicated to all aspects of primatology, was first founded in 1976, it has been committed to advancing primate conservation. In 1989, the ASP initiated a Conservation Small Grant program to provide small awards (usually ranging from \$500 to \$1,500 per award) to support research and education-based projects with a clear goal of contributing to primate conservation (Kyes and Howell 1999). Although the grants are generally small, they do represent an important source of funding for habitat country nationals and graduate students from around the world. The program is also competitive; from 2011–2015, a mean of 21.6% (±2.79) of applicants were successful. To our knowledge, however, there has been no attempt to evaluate the success of the program in effecting primate conservation since its inception. To begin to fill this gap in knowledge, we developed and administered a survey to former grant recipients from the years 1997-2012 to assess whether the ASP funded projects had resulted in further research, dissemination of results, capacity building and other conservation outcomes. In order to contribute to a "safe-fail culture in conservation" (Redford and Taber 2000; p.1567) that exposes both what works and what doesn't, we also assessed grant recipients' perceptions regarding factors that impeded conservation outcomes and those that would have facilitated greater success.

Methods

We used a voluntary survey instrument administered to former grant recipients (from 1997–2012) via email to assess

conservation impact. The survey was developed in the fall of 2012 and approved by the ASP Board of Directors in January 2013. The Institutional Review Board (IRB) at San Diego State University determined that human subjects' approval was not required to administer the survey. The survey comprised 10 questions (Table 1). We used the online service SurveyMonkeyTM to create the survey and collect responses. We sent the survey link via email to former grant recipients for whom we could find current contact information (106 people out of a total of 185). The survey link was made available from April-September 2013. We acknowledge that our approach relied on self-assessment and hence is inherently subjective and potentially subject to bias. At the same time, project personnel are likely the best sources of information on the implementation and outcomes of their project (Kapos et al. 2008).

Table 1. Survey questions asked to ASP Small Grant recipients.

- What was the title of your ASP funded project? (Please include species/ taxa, and whether the study was research or education based)
- 2. What was your institutional affiliation at the time of your ASP funded project?
- 3. What is your current institutional affiliation?
- 4. Other than the report required to be submitted to ASP for publication in the Bulletin, were the results from your ASP funded project published? If yes, where and when?
- Were your results disseminated in another way? If yes, how? If no, why not?
- 6. Did your ASP funded project lead to further research? If yes, please explain and indicate whether research is currently on-going.
- Did your ASP funded study result in capacity building (e.g., training of park personnel, career development for habitat country nationals)? Please explain your answer.
- 8. What are some specific conservation outcomes that resulted either directly or indirectly from your ASP funded project?
- 9. What factors may have impeded conservation outcomes resulting from your project?
- 10. What factors may have helped your project be more successful in generating conservation outcomes?

Results

Characteristics of all ASP funded projects, 1989–2015

To date, the ASP Conservation Small Grant program has funded 185 projects on 74 primate species in 41 countries. The geographic coverage of the projects is fairly evenly spread across Africa, Asia, and the Neotropics (Fig. 1a). The majority of projects have been research-based (87%), with the majority focusing on Old World and New World monkeys, followed by apes and then prosimians (Figs. 1b and 1c). The conservation status of the target species varied across the IUCN categories, but the majority (68%) were classified as "Threatened with Extinction" (i.e., Critically Endangered, Endangered, and Vulnerable) (Fig. 1d).

Characteristics of our survey sample, 1997–2012

Of the 106 people we contacted, 42 responded, resulting in a 39.6% response rate. Survey respondents were involved in projects in 19 countries, focusing on 26 primate species. The geographic coverage of survey respondent projects is also fairly evenly spread across the world regions (Fig. 2a). The majority of projects were research-based (83%) and focused on Old World and New World monkeys (Figs. 2b and 2c). The majority (81%) of survey respondents were affiliated with an academic institution at the time of the funded project. The IUCN conservation status of the target species varied across the categories, but the majority (65%) were classified as "Threatened with Extinction" (Fig. 2d). Although the response rate is low and our sample size is rather small, the breakdown of this sample is representative of the total pool of ASP grant recipients (Figs. 1 and 2).

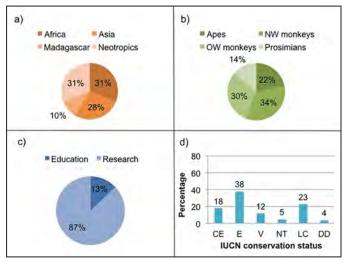


Figure 1. Descriptives on all ASP Conservation Small Grant projects (1989–2015): Percentage of projects by (a) geographic region, (b) taxonomic category, (c) focus, and (d) IUCN conservation status of all species involved in ASP funded projects (CE = Critically Endangered, E = Endangered, V = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient).

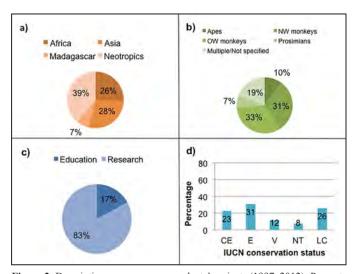


Figure 2. Descriptives on survey respondents' projects (1997–2012): Percentage of projects by (a) geographic region, (b) taxonomic category, (c) focus, and (d) IUCN conservation status of target species (CE = Critically Endangered, E = Endangered, V = Vulnerable, NT = Near Threatened, LC = Least Concern).

Dissemination and further research

Almost all respondents (93%) disseminated their results in some way, such as in printed sources, digital media, social media, and oral presentations (for example, theses and dissertations, newspapers, local radio, local TV, and presentations to local schools and communities). Approximately half of the survey respondents reported publishing their project results in a peer-reviewed scholarly journal. The top three journals noted as venues for papers based on ASP funded projects are American Journal of Primatology, International Journal of Primatology, and Folia Primatologica. The percentage of those who published papers increases to 64% if book chapters are included. Out of the number of respondents who conducted research-based projects, 89% reported that their ASP funded project led to further research. This additional research took the form of new but related projects conducted by the grant recipient, follow-up research conducted by subsequent students, and the continuation of long-term studies.

Capacity building

Eighty-one percent of respondents reported that their ASP funded projects led to at least one form of capacity building, and 12% of respondents reported multiple examples. Capacity building occurred at the personal (for example, researcher career growth), educational (for example, student and field assistant training and employment), community (for example, training and employment of local teachers, park staff, government officials, and community members), and organizational levels (for example, project evaluation) (Table 2). The most frequently reported examples of capacity building were the training and employment of students (n = 17) and local people (n = 11) (bolded in Table 2).

Other conservation outcomes

The majority of survey respondents (79%) reported at least one conservation outcome (beyond dissemination of results and capacity building) that resulted from their project. Conservation outcomes fell into the following five categories: (1) building conservation awareness and knowledge, (2) building institutional and infrastructural support, (3) building critical datasets, (4) augmenting enforcement efforts, and (5) enhancing primate habitats (Table 3). The two most frequent responses were: research presence generates greater local awareness/interest in target species and/or its habitat and increased scientific understanding of target species (bolded in Table 3).

Factors impeding conservation outcomes

Sixty-four percent of respondents reported at least one factor that impeded conservation outcomes. Reported obstacles to conservation success were political, financial, practical, academic, cultural, and educational in nature. The top five factors impeding conservation outcomes were (1) limited funding, (2) limited time, (3) illegal resource extraction, (4) changes in local government, and (5) lack of support from

local people. Additional examples of challenges to conservation success included problematic volunteers, rugged terrain, and language barriers.

Table 2. Types of capacity building reported by grant recipients.

Category	Туре	# of times reported
Personal	Researcher career growth	2
Educational	Student/research assistant training	17
	Employment for trained students/field assistants	5
Local community	Training and employment of local people	11
	Training of national park staff	4
	Teacher training	1
	Education of government officials	1
	Education of local students and community members	2
Organizations	Opportunity for organization to evaluate	1
	projects	1
	Establishment of training program for organizations/universities/government	

Table 3. Conservation outcomes reported by survey respondents.

Category	Outcome	# of times reported
Building conservation awareness and	Research presence generates greater lo- cal awareness/interest in target species/ habitat	8
knowledge	Establishment and continuation of local education programs	3
	Evaluating conservation efforts	2
	Study species became a flagship species	1
	Informative signs established in protected areas	1
	Holding of annual conservation workshops	1
Building insti-	Established strong contact networks	3
tutional and infrastructural	Increased publicity/visibility for projects/ organizations	3
support	Training of students/employees	3
	Established new conservation organization	2
	Building of ongoing research site	2
	Establishment of local environment committee	1
	Building of education center	1
Building criti- cal datasets	Increased scientific understanding of the target species	9
	Established baseline data	3
	Contributions to larger/existing datasets	4
Augmenting	Increased patrols for illegal activity	2
enforcement efforts	Increased monitoring of protected area	2
CJJOI IS	New hunting restrictions	1
	Research presence deters poaching	1
Enhancing pri- mate habitats	Establishment of successful wildlife bridges and/or natural corridors	2

Factors to improve conservation success

When asked about factors that would have increased conservation success, the respondents' most frequent suggestions were developing partnerships with local NGOs and governments, establishing a long-term research presence, and securing follow-up funding (Fig. 3). Other responses included increased communication with and more support for protected area staff, increased involvement of students and local people, and more time to implement result-based strategies.

Discussion

For more than 25 years, the ASP has been providing small grants in support of research and education-based projects aimed at effecting the conservation of nonhuman primate populations. Our objective was to begin to assess the conservation impact of this grant program, and ultimately, to provide critical "lessons learned" information to help improve the effectiveness of primate conservation small grant programs like that of ASP. The results indicate that the ASP small grant program primarily supports indirect conservation activities (for example, education and awareness building, capacity building, and increasing scientific understanding). While improved status of the target species may be the ultimate outcome (and measure) of the conservation success (impact) of a project, conservation practitioners and scholars acknowledge that such a result often requires considerable time depth as "biological outcomes often respond slowly to interventions" (Ferraro and Pattanayk 2006; p.486). Accordingly, evaluation efforts should also focus on basal outcomes (for example, enhanced conservation skills of field assistants in a capacitybuilding project) that can result in intermediate or "key" outcomes (for example, improved quantity or quality of conservation action as a result of capacity building) (Kapos et al. 2010). Intermediate outcomes are typically easier to measure than changes in the target species' status and the threats it faces, and have been found to be useful predictors of the likelihood of the species' persistence (Kapos et al. 2008, 2010). Although our results indicate that ASP funded projects have largely produced basal outcomes, some intermediate outcomes are also apparent (for example, increased enforcement efforts and the application of research results in conservation practice such as through the building of habitat corridors to improve dispersal).

The finding that no respondents reported ultimate outcomes (i.e., improved species status) may be explained by a number of factors (beyond the underlying constraint that such outcomes often require lengthy periods). The majority of ASP grant recipients are affiliated with academic institutions which means they likely have additional responsibilities (for example, completion of a dissertation, high publication expectations, full-time teaching and heavy service loads), thereby making it difficult to ensure the generation of intermediate and ultimate outcomes. Referred to as the "great divide" between theory and practice (Anonymous 2007), researchers in academia are often accused of "knowing, but not doing" (Knight *et al.*



Figure 3. A Wordle™ word cloud generated from responses regarding how to improve conservation success.

2008; Arlettaz et al. 2010). This "lack of time" constraint, frequently noted by respondents, is exacerbated by the reality that academic institutions tend to value basic research leading to publications over applied work, such as the implementation of conservation actions (Meffe 1998; Chapron and Arlettaz 2008; Arlettaz et al. 2010). Another possible explanation is that the small size of the ASP grants does not effectively enable recipients to generate intermediate or ultimate outcomes. Therefore, for small grant programs such as that of ASP with limited funds, the evaluation of basal outcomes may be a more realistic measure of conservation impact. The fact that the majority of ASP grant applicants disseminated their results and led to capacity building through the training of students and local people who may in turn continue working in conservation is promising (cf. du Plessis and Primack 2001). There is also clear evidence of multiple projects having a lasting impact in the form of establishing a long-term presence in an area, thereby facilitating ongoing research.

Our results also generate a number of important lessons for primate conservation activities in general and the small grant programs that fund them. First, the survey results provide further support that partnerships with other institutions, such as local conservation NGOs, and the support of local people are recognized as critical to the success of conservation projects (Ancrenaz et al. 2007; Méndez-Carvajal et al. 2013; see also Mariki et al. 2015). Second, our results raise the important question of whether the likelihood of conservation success will be greater at sites where a long-term research presence exists (Pusey et al. 2007). For example, Campbell et al. (2011) empirically demonstrated that encounter rates of primates and duikers in Taï National Park, Côte d'Ivoire, were higher in the research area compared to adjacent areas, thereby supporting the assumption that a research presence effectively protects wildlife by reducing hunting pressure. Sustained research presence may therefore be an important

criterion for grant programs to consider when deciding which projects to fund. Third, the results indicate that within the conservation community there is a lack in consistency in the use of key conservation terms such as "outcomes," "actions," and "outputs." For instance, while some may see the development of informative signs as an output (cf. Ferraro and Pattanyak 2006), others may envision it as a specific conservation outcome. It is therefore critical that the primate conservation community work collectively to clearly define terms to ensure clear and efficient monitoring and evaluation (see Stem et al. 2005). Along with having clearly defined terms, our project reinforces the need for researchers to build evaluation into the design of their projects (Ferraro and Pattanyak 2006), and for grant programs like ASP's to stipulate the linking of actions and outcomes in grant applications (Kapos et al. 2008). For example, if a proposed project aims to develop a conservation education program (action), the design could also include attention to assessing changes in people's behavior as a result of the education program (outcome). A final lesson learned concerns the important issue of hesitancy in reporting project shortcomings. Admittedly, we were surprised that so many of the survey respondents in our study were willing to discuss the specific factors that impeded success of their projects, given the general reluctance in the overall conservation community to share less successful experiences (Kapos et al. 2010). We should encourage and enable scholars and practitioners alike to share their successes as well their failures (see, for example, Webber et al. 2007), as such information is critical for the design, implementation, and assessment of future primate conservation endeavors.

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The Distribution and Taxonomy of Titi Monkeys (*Callicebus*) in Central and Southern Peru, with the Description of a New Species

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Abstract: Here we report on the results of a study on the distribution and taxonomy of titi monkeys, genus *Callicebus*, in the central part of Peru. We reinstate *Callicebus toppini* Thomas, a species described in 1914, but since then neglected by science. It evidently has a wide distribution in southern Peru, western Brazil and northern Bolivia. Based on field observations, analysis of museum specimens, and photographs, we also describe a new species of *Callicebus* from the Río Urubamba basin, endemic to Peru. Reliable identification of titi monkeys observed in the wild is crucial to avoid confusion and to determine conservation strategies.

Key Words: Callicebus, distribution Peru, Platyrrhini, Primates, taxonomy

Introduction

More than 50 titi monkeys have been described since Hoffmannsegg's descriptions of *Cebus moloch* and *Callitrix torquatus* in 1807. Through the years, many have been synonymized, and the latest revision of the genus by Van Roosmalen *et al.* (2002) listed just 26 species. They described two more species, *C. bernhardi* and *C. stephennashi*, from the Brazilian Amazon, and a further four species have been newly described since then—*Callicebus aureipalatii* Wallace *et al.*, 2006, from Bolivia; *Callicebus caquetensis* Defler *et al.*, 2010, from the Colombian Amazon; and *Callicebus vieirai* Gualda-Barros *et al.*, 2012, and *Callicebus miltoni* Dalponte *et al.*, 2014, from the Brazilian Amazon. This brought the total to 32 species, and more are awaiting scientific description (Araújo 2013; Van Roosmalen and Van Roosmalen 2014).

The taxonomy and distributions of the Peruvian titi monkeys are still poorly understood. Hershkovitz (1990) listed six species in Peru (*oenanthe*, *brunneus*, *cupreus*, *discolor*, *caligatus* and *lucifer*). The presence of *C. caligatus* is questionable (Aquino and Encarnación 1994; Van Roosmalen *et al.* 2002), and may be based on a misidentification of museum specimens (Voss and Emmons 1996). Titis belonging to a possibly undescribed species have been reported from northern Peru (Aquino *et al.* 2008). Three other Peruvian *Callicebus* have been described, but these Hershkovitz (1990) considered to

be junior synonyms of *C. cupreus* (*C. toppini* Thomas, 1914) or *C. discolor* (*C. subrufus* Elliot, 1907; *C. rutteri* Thomas, 1923); a viewpoint followed in subsequent revisions (Aquino and Encarnación 1994; Van Roosmalen *et al.* 2002). The species' distributions proposed by Hershkovitz (1990), Aquino and Encarnación (1994) and Van Roosmalen *et al.* (2002) are based on few museum specimens and sometimes even fewer field studies. Recent field surveys by Bóveda-Penalba *et al.* (2009) and Vermeer *et al.* (2011) have resulted in extensions of the known distributions of *C. oenanthe* and *C. discolor*, respectively.

The area around Atalaya, Ucayali Department, central Peru, is of the utmost interest for primate taxonomy. The Río Urubamba (flowing from the south), the Río Tambo (flowing from the west) and the Río Inuya (flowing from the east) come together near Atalaya and continue their course northwards as the Río Ucayali (Fig. 7). The ríos Urubamba, Ucayali and Tambo are believed to serve as geographical barriers for delimiting the ranges of primate species (Hershkovitz 1990; Aquino and Encarnación 1994; Aquino *et al.* 2013). The upper Río Inuya is known locally for its abundance of primates, which, however, are threatened by hunting and logging.

Our understanding of the distributions and taxonomy of titi monkeys around Atalaya is based mainly on a collection of specimens made by the Olalla brothers in 1927 (Wiley 2010),

now preserved in the collection of the American Museum of Natural History (AMNH); 22 specimens of three different species of titi. The dark brown specimens, labeled "Mouth Río Inuya, Río Urubamba" or "Boca Río Urubamba," were identified by Hershkovitz (1990) as belonging to *Callicebus brunneus*. Hershkovitz (1990) identified the reddish specimens with a dark forehead, labeled "Mouth Río Urubamba" or "Mouth Río Inuya," as *Callicebus cupreus cupreus*, and the reddish animals with a white blaze, from "Boca Río Inuya" and "Lagarto," as *Callicebus cupreus discolor*.

In his map, Hershkovitz (1990, p.53) placed the range of discolor on the left bank of the Río Ucayali and that of cupreus on the right bank as well as on both sides of the Río Inuya. He mentioned that C. brunneus might occur in the Peruvian departments of Madre de Dios, Puno and Cusco, but questioned the provenance of AMNH specimens labeled as coming from the Río Inuya and Río Urubamba (in the Ucayali Department). Aquino and Encarnación (1994) followed Hershkovitz regarding the distributions of C. discolor and C. cupreus, and added that the range of C. brunneus extends from the upper Río Purús in Ucayali Department south to the Bolivian border. Van Roosmalen et al. (2002) also agreed regarding the distributions of C. discolor and C. cupreus, but restricted the range of C. brunneus on their map (p.5) to the east of the Río Madeira. Confusingly, their accompanying text mentions that "in the west of its distribution, it is parapatric with C. cupreus along the upper Río Purús," which is not possible if the species is indeed restricted to east of the Río Madeira, while the Río Purus is west of the Río Madeira. Since then, several authors have reported the presence of C. brunneus in southern Peru (Philips et al. 2004; Solari et al. 2006; Palminteri et al. 2009).

Hershkovitz (1990) described C. brunneus as a species with the upper parts and sides of the body brownish agouti, underparts brownish or reddish brown, and forehead, forearms, legs, hand and feet blackish. This matches very well the original description of the species (Wagner, 1842), except that Wagner described it as being chestnut-brown. Van Roosmalen et al. (2002) caused confusion by picturing C. brunneus with reddish underparts and a buffy tail; their photographs show in fact C. cupreus. This was corrected by Vermeer (2009), but as Hershkovitz (1990) had mentioned that the southern departments of Peru are inhabited by C. brunneus, it is possible that researchers without thorough knowledge of taxonomy simply assumed that all titi monkeys encountered in southern Peru were C. brunneus (Philips et al. 2004; Solari et al. 2006; Palminteri et al. 2009), even if the animals were reddish (probably following Van Roosmalen et al. 2002).

A species that warrants extra attention is the earlier mentioned *Callicebus toppini*. The type locality is the Río Tahuamanu, in south-eastern Peru (not north-eastern; a *lapsus calami* by Thomas 1914). Hershkovitz (1963) first considered *C. toppini* to be a junior synonym of *C. brunneus*, but after examining more specimens, including the holotype, in his 1990 revision he synonymized it with *C. cupreus*. Partly based on the examination of the AMNH specimens from the Atalaya area, he included the Río Inuya within the range of

C. cupreus. However, the AMNH specimens from the Atalaya region all have dark tails with a whitish tip, and match well the original description and the holotype of *C. toppini* (J. Vermeer, pers. obs.). There is no apparent geographical boundary between the type locality and the Río Urubamba.

In this paper we report the results of an expedition to the Atalaya region, Ucayali Department, Peru. The goal was to identify the species of *Callicebus* living in the region and to determine their distributions. We reinstate *Callicebus toppini* as a valid taxon, phenotypically distinguishable from *C. cupreus*, with which it was synonymized for many years. The species has an extensive distribution throughout southern Peru, western Brazil and north-western Bolivia. We also describe a new species from the Río Urubamba, recognizable by its brown color and black face, and known with certainty from only a few localities. We provide images of the different species living in southern Peru and their hypothetical distributions to facilitate the identification of titi monkeys by other investigators.

Methods

Study sites

We carried out surveys for six weeks in November and December 2013 along the ríos Urubamba, Inuya and Ucayali in the area around Atalaya. The study was conducted in three sectors, thereby obtaining a good knowledge of the overall distribution of the different species and the role of the rivers as barriers for titi monkey distributions. We walked 144 km of trails and surveyed 169 km by canoe.

Sector 1: both margins of the Río Inuya. The Río Inuya is on the right bank of the Río Urubamba. We conducted surveys for nine days on both sides of the river. Some of the observations were done on forest trails, while other titi monkeys were observed during river surveys. The forest can be described as open primary forest, with "pacales" (areas of spiny bamboo, Guadua).

Sector 2: both margins of the Río Urubamba. During the 11 days we spent along the Río Urubamba, most were devoted to the left bank, as the right bank was already included in the Sector 1 surveys. Most of our observations were along existing trails, but we also made a number of observations along the Río Sepa, a narrow and shallow river flowing eastwards into the Río Urubamba. The forest close to the river is comparable to that along the Río Inuya, but there is more human disturbance and most observations were made in regenerating secondary forest.

Sector 3: both margins of the Río Ucayali. The forest along the Río Ucayali is denser, with taller trees than in the southern study areas. However, there are more settlements and disturbance is very high. During the ten days in this sector, we walked many existing trails on both banks of this wide river, but also used our boat to enter some of its smaller tributaries, Quebrada Chicosillo and Quebrada Shebonillo. Pacales are practically absent and much of the area is flooded during the wet season.

Field surveys

During our study, we applied three different methods that have proven to be successful during surveys in other parts of Peru; interviews with local people, listening to vocalizations, and direct observations. However, owing to resemblances in coloration and vocalizations between the different species, we have concentrated on direct observations for our results and conclusions.

Titi monkeys are discreet animals that are difficult to find in the forest. They advertise their presence in the morning by loud vocalizations that probably serve to define the boundaries of their territories (Robinson 1979; Aldrich *et al.* 2008). In order to stimulate titi monkeys to call, we played recordings of different *Callicebus* species in the hope that they would answer and approach us. This method has been used successfully by other researchers (Rowe and Martinez 2003; J. Lawrence, pers. comm.). If titi monkeys were heard calling, we tried to find them. When possible, we filmed and photographed the titis and recorded their vocalizations. We conducted interviews at each locality where people were present. No transects were opened up for this study, and we used solely existing trails and rivers.

No animals were killed for our study. We encountered hunters with dead titi monkeys, however, and took the opportunity each time to obtain skins and skulls. All specimens obtained are listed below and were deposited in the Natural History Museum of Lima (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos).

Results

Sector 1: Río Inuya

We saw titi monkeys at 14 localities along the Río Inuya, and heard them at three other sites. On only one occasion were we unable to identify the species observed; they disappeared into the vegetation as soon as we arrived. The 29 individuals that we observed on both sides of the river showed little color variation. They had reddish undersides and cheeks, a greyish back, a yellowish crown and a dark tail with a whitish tip. We identified these animals as being *Callicebus toppini* (see discussion). We walked 62 km of trails and surveyed 81 km of river banks.

Sector 2: Río Urubamba and Río Sepa

We encountered titi monkeys at 14 localities along the Río Urubamba and its tributary, the Río Sepa. Titis were also reported at another locality. The titi monkeys observed at all localities on the left (western) side of the Río Urubamba were very dark, brownish with black forearms, hands, feet and face. They were easily distinguishable from the titis along the Río Inuya. No variation was detected among the 35 individuals that we encountered. These titis are a new, previously undescribed species (see discussion). We obtained the skin and skull of a dead specimen shot for food by a hunter.

Animals of the reddish species, *C. toppini*, were observed at the locality that we surveyed on the right bank of the Río Urubamba. Having heard the sound of gunfire, we met a hunter

who had just killed two titis (an adult male with infant). He allowed us to remove their skins and skulls (Figs. 1–6). Titis clearly resembling *C. toppini* were also reported at another locality on the right bank of the Río Urubamba. We walked 38 km of trails and surveyed 49 km by canoe.

Sector 3: Río Ucayali

We encountered titi monkeys at 13 localities along the Río Ucayali and we heard them at two. The situation along this river is different from that reported in the literature (Hershkovitz 1990; Aquino and Encarnación 1994). At four localities on the right bank of the Río Ucayali, in its southern reaches, we encountered 16 titis that were similar to the reddish titi monkeys along the Río Inuya, which we identified as *C. toppini*. At one point (near latitude 10°2'50"S), this species was replaced by a different titi that had a white stripe on the forehead, reddish underparts, a brownish back, and a tail with the terminal half whitish. We observed this species at four localities (22 individuals) and it was reported at an additional locality on the same side of the river. The species was identified as *Callicebus discolor* (sensu lato).

We found no evidence of titi monkeys in the area just north of the Río Tambo, on the left bank of the Río Ucayali. It was not clear to us if this was a natural absence or that the species had been extirpated. We encountered more titis, matching the phenotype of *Callicebus discolor* that we had also observed on the other river bank, at three localities (nine individuals) to the north of this area. We walked 44 km of trails surveyed 39 km by canoe. The results are summarized in Figure 7 and Table 1.

Discussion

The goal of this study was to identify the different species of *Callicebus* in the Atalaya region and to determine their distributions. During the expedition we encountered three species, including one which was new and undescribed. The three species are discussed here and we indicate their hypothetical distributions.

Callicebus toppini Thomas, 1914

Callicebus toppini. Thomas, O. 1914. Ann. Mag. Nat. Hist., 8th ser., 13: 480. Toppin's titi. Type locality. Río Tahuamanu, N. E. Peru [sic], near Bolivian boundary. About 12°20'S, 68°45'W. Synonym: Callicebus cupreus acreanus Vieira, C. da C. 1952. Pap. Avuls. Dept. Zool., São Paulo (11): 23. Acre titi. Type locality. Brazil: Iquiri, Territory of Acre, upper Rio Purus.

The reddish, dark-tailed titi monkeys that we encountered on the right (eastern) side of the Río Urubamba and the upper Río Ucayali did not match *C. cupreus* (Fig. 8), *C. discolor* or *C. brunneus* that have been reported in recent taxonomic revisions (Hershkovitz 1990; Van Roosmalen *et al.* 2002) as occurring in the central and southern part of Peru. After studying the literature and the holotype at the British Museum



Figures 1–3. (left column) Lateral and frontal views of the head, and ventral view of the specimen of *C. toppini* collected on the right bank of the Río Urubamba (specimen deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42399). Note the reddish hairs on the ears, thin black line on the forehead and yellowish crown. Photographs by Proyecto Mono Tocón.





Figures 4 and 5. (above) Dorsal views of the specimen of *C. toppini* MUSM 42399 collected on the right bank of the Río Urubamba. Photographs by Proyecto Mono Tocón.

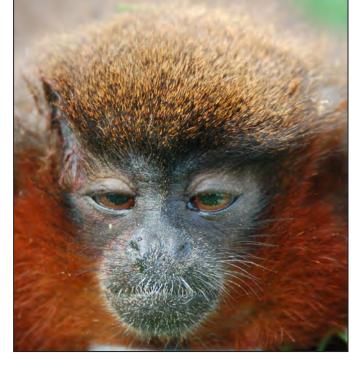






Figure 6. (above) The infant of *C. toppini* is uniformly reddish-agouti dorsally, comparable to the coloration of infants of *C. cupreus*. Specimen collected on the right bank of the Río Urubamba (deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42400). Photograph by Proyecto Mono Tocón.

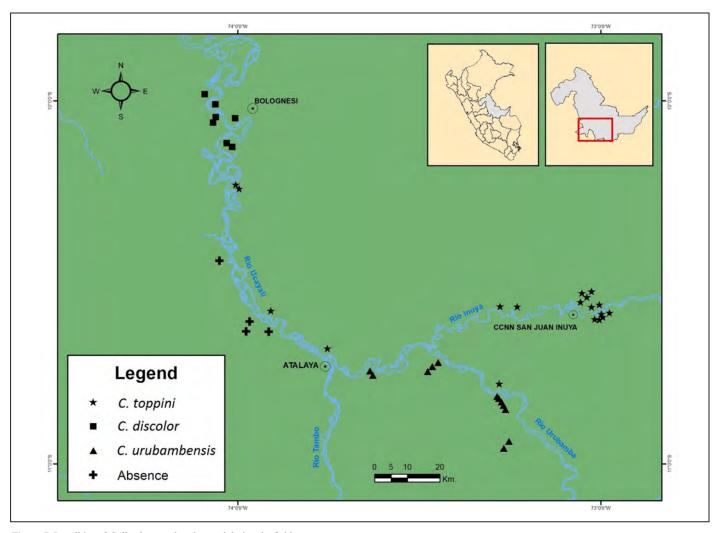


Figure 7. Localities of Callicebus species observed during the field survey.

Table 1. Localities, number of individuals seen and identification of *Callicebus* observed during the field survey.

Locality	River / M	argin	Altitude (m)	Taxon	Number of individuals seen	Coore	linates
Río Ucayali	Ucayali	Right	180	C. discolor	4	10°02'50"S	74°00'26"W
Quebrada Shebonillo	Ucayali	Left	208	C. discolor	5	10°02'13"S	74°03'34"W
Quebrada Shebonillo	Ucayali	Left	178	C. discolor	2	10°02'26"S	74°03'35"W
Betijay	Ucayali	Right	175	C. discolor	*	10°02'08"S	74°02'25"W
Río Ucayali	Ucayali	Right	187	C. discolor	7	10°00'09"S	74°04'30"W
Río Ucayali	Ucayali	Left	173	C. discolor	2	09°59'15"S	74°05'02"W
Río Ucayali	Ucayali	Right	199	C. discolor	5	10°06'16"S	74°01'42"W
Río Ucayali	Ucayali	Right	173	C. discolor	6	10°06'21"S	74°01'30"W
Río Sepa	Sepa	Left	264	C. urubambensis	4	10°57'20"S	73°15'50"W
Río Sepa	Sepa	Right	296	C. urubambensis	5	10°56'26"S	73°15'19"W
Penal del Sepa	Urubamba	Left	267	C. urubambensis	3	10°48'45"S	73°17'15"W
Penal del Sepa	Urubamba	Left	269	C. urubambensis	3	10°48'47"S	73°17'12"W
Penal del Sepa	Urubamba	Left	268	C. urubambensis	3	10°48'49"S	73°17'10"W
Penal del Sepa	Urubamba	Left	258	C. urubambensis	3	10°48'45"S	73°17'14"W
Penal del Sepa	Urubamba	Left	280	C. urubambensis	3	10°48'50"S	73°17'08"W
Takile	Urubamba	Left	253	C. urubambensis	2	10°43'03"S	73°26'47"W
Takile	Urubamba	Left	267	C. urubambensis	4	10°43'20"S	73°27'08"W
Takile	Urubamba	Left	227	C. urubambensis	1	10°43'13"S	73°27'03"W
San José	Urubamba	Left	306	C. urubambensis	2	10°44'31"S	73°38'12"W
San José	Urubamba	Left	301	C. urubambensis	2	10°44'29"S	73°38'18"W

Table 1 continued on next page

Table 1. (continued)

Locality	River / M	argin	Altitude (m)	Taxon	Number of individuals seen	Coord	dinates
San Juan/Inuya	Inuya	Right	267	C. toppini	2	10°34'27"S	73°00'22"W
San Juan/Inuya	Inuya	Right	256	C. toppini	3	10°34'44"S	73°01'36"W
San Juan/Inuya	Inuya	Right	331	C. toppini	1	10°33'13"S	73°03'22"W
San Juan/Inuya	Inuya	Right	282	C. toppini	3	10°31'51"S	73°02'58"W
San Juan/Inuya	Inuya	Right	308	C. toppini	1	10°31'57"S	73°02'25"W
San Juan/Inuya	Inuya	Right	301	C. toppini	1	10°31'58"S	73°02'30"W
San Juan/Inuya	Inuya	Left	252	C. toppini	1	10°34'10"S	73°00'20"W
San Juan/Inuya	Inuya	Left	274	C. toppini	3	10°34'26"S	73°00'22"W
San Juan/Inuya	Inuya	Left	265	C. toppini	1	10°34'19"S	73°00'19"W
San Juan/Inuya	Inuya	Right	315	C. toppini	4	10°34'36"S	72°59'06"W
San Juan/Inuya	Inuya	Left	265	C. toppini	4	10°34'35"S	72°59'36"W
Río Inuya	Inuya	Right	250	C. toppini	2	10°35'04"S	73°14'38"W
Río Inuya	Inuya	Left	241	C. toppini	3	10°34'38"S	73°16'52"W
Quebrada Chicosillo	Ucayali	Right	216	C. toppini	2	10°40'54"S	73°45'11"W
Río Ucayali	Ucayali	Right	208	C. toppini	5	10°35'27"S	73°55'12"W
Río Ucayali	Ucayali	Right	188	C. toppini	4	10°13'43"S	74°00'38"W
Río Ucayali	Ucayali	Right	196	C. toppini	5	10°13'47"S	74°00'34"W
Río Urubamba	Urubamba	Right	260	C. toppini	3	10°47'25"S	73°16'43"W
Sabaluya	Urubamba	Right	240	C. toppini	*	10°41'05"S	73°42'07"W

^{*} no observation, but presence reported by local communities



Figure 8. Toppin's titi, *Callicebus toppini* (left) compared to the coppery titi *Callicebus cupreus* that has a fluffier tail that is more whitish throughout its length (on the right). Some *C. cupreus* are as orange as *C. toppini*, but always have a whitish tail. Illustrations by Stephen D. Nash.

(Natural History) in London (Figs. 9–11), we identified the observed and collected reddish animals as *Callicebus toppini*.

This species was described by Thomas (1914; p.480) as follows: "Allied to and of the same grizzled brown color as *C. cupreus*. Crown-hairs similarly tipped with buffy, but along the front edge of the hairy part of the forehead the hairs are black, thus forming an indistinct blackish frontal band. Belly and terminal part of limbs red, as in *cupreus*, but on the hind legs the red is rather more extended, coming up to cover the knee. Hairs on ears dark reddish brown, tail hairs mixed







Figures 9–11. Holotype of *Callicebus toppini* in the British Museum (Natural History). Collection no. BM 19.14.3.3.3. Photographs courtesy of the British Museum (Natural History) Picture Library.

grey and blackish, as in *cupreus*, but those on the proximal two-thirds are tipped with black, not with white or buffy as in the other species of this group." The type locality is the Río Tahuamanu, in south-eastern Peru (Fig. 24).

Hershkovitz (1963) first considered *C. toppini* to be a junior synonym of *C. brunneus*, but after examining more specimens, including the holotype, in his 1990 review he synonymized it with *C. cupreus*. Partly based on the examination of the AMNH specimens from the Atalaya area, he included the Río Inuya in the range of *C. cupreus*. The AMNH specimens from the Atalaya region all have dark tails with a whitish tip, and match well with the original description and the holotype of *C. toppini* (J. Vermeer pers. obs.).

A comparable dark-tailed taxon, *acreanus* Vieira, from Iquiri, Acre, Brazil, closely resembles the holotype of *C. toppini*, and we consider it to be a junior synonym, as did Cabrera (1957). Examination of pictures of animals from the eastern part of Manu (and our observations of live animals), Los Amigos, Río Camisea and the Tambopata National Reserve in Peru, from Acre in Brazil and from the Pando in Bolivia (see also Rowe and Martinez 2001; Martinez and Wallace 2013; Porter *et al.* 2013) indicates that this whole area is occupied by *Callicebus toppini*. There may be some intraspecific variation in coloration, mainly on the ventrum, and the amount of black hairs on the forehead, ears or hands (Figs. 12–23). In our opinion, the variation seen is not geographically consistent or significant enough to consider the presence of different species.

Table 2. Cranial measurements (mm) of the collected *C. toppini* specimen adult male MUSM 42399, deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima. After Kobayashi (1995).

Cranial measurement	Adult male
Nasion – Rhinion	9.2
Rhinion – Prosthion	11.39
Nasion – Prosthion	20.6
Left maxillofrontale -Right maxillofrontale	3.81
Left frontomalare orbitale -Right frontomalare orbitale	29.85
Left zygomaxillare superior -Right zygomaxillare superior	27.45
Left frontomalare orbitale - Left zygomaxillare superior	11.15
Left zygomaxillare superior -Left zygomaxillare inferior	14.52
Greatest width across outer margins of orbit	34.29
Left zygion - Right zygion	37.95
Greatest width across narrowest part in postorbital portion	30.45
Left euryon - Right euryon	33.97
Prosthion - Bregma	44.47
Nasion - Bregma	29.08
Bregma - Lambda	30.13
Prosthion - Lambda	57.96
Basion - Bregma	33.63
Left zygomaxillare inferior -Right zygomaxillare inferior	32.3
Left kondilion laterale - Right kondilion laterale	32.01
Left koronion - Right koronion	37.22
Infradentale -Left kondilion laterale	38,93
Infradentale - Gnathion	12.97
Greatest length between left koronion and base of mandibular	32.31







Figures 12–14. Callicebus toppini from three different localities. From left to right: Manu National Park, on the border of the upper Río Madre de Dios, Peru (photo by Mauro Mozzarelli); Los Amigos, north of the Río Madre de Dios, Peru (photo by Job Aben); and Tambopata Research Center, left margin of the Río Tambopata and south of the Río Madre de Dios, Peru (photo by Inés Nole Bazán). For localities, see Figure 24.







Figures 15–17. Callicebus toppini from two localities. On the left a titi from the left side of the Río Inuya, Peru (photo by Proyecto Mono Tocón); in the middle a male from the Los Amigos Biological Station (CICRA), north of the Río Madre de Dios, Peru (photo by Cédric Girard-Buttoz), and on the right a titi killed by hunters near Los Amigos (photo by Jenna Lawrence). The latter two have very dark hands and feet compared to other animals on the pictures (including other animals from the same locality, Fig.13). For localities, see Figure 24.







Figures 18–20. Callicebus toppini from the Tambopata Research Center, left bank of the Río Tambopata, south of the Río Madre de Dios, Peru (photos from left to right by: Brett Cole, Roland Seitre and Peter Eekelder). For localities, see Figure 24.







Figures 21–23. Three more *Callicebus toppini* from Brazil and Bolivia. From left to right: Zoobotanical Park of the Federal University of Acre, Río Branco, Acre, Brazil (photo by J. C. Bicca-Marques); Río Branco, Brazil (photo by Tomaz Nascimento de Melo), and Manuripi, Pando, Bolivia (photo by Erwin van Maanen). For localities, see Figure 24.

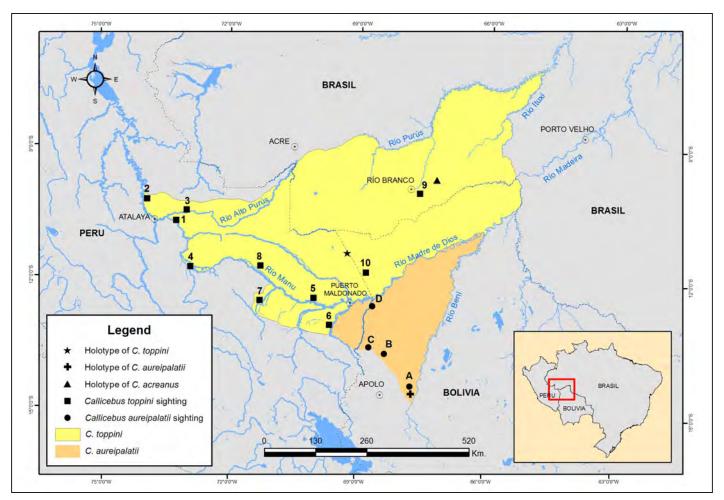


Figure 24. Hypothetical distributions of Toppin's titi *Callicebus toppini* and the Madidi titi *Callicebus aureipalatii*, based on observations, photographs, examination of museum specimens and literature cited in the text. Locality 1: Rio Urubamba, Peru (this study); 2: Río Ucayali, Peru (this study); 3: Río Inuya, Peru (this study); 4: Río Camisea, Peru (pictures provided by T. Gregory); 5: Los Amigos, Peru (Figs. 13, 16, 17, and many other pictures); 6: Tambopata Research Center, Peru (Figs. 14, 18, 19, 20, and many other pictures); 7: Manu National Park, upper Río Madre de Dios, Peru (Fig. 12, and pers. obs.); 8: Manu National Park, Cocha Cashu, Peru (pictures provided by John Bunce and Inés Nole Bázan); 9: Río Branco, Acre, Brazil (Figs. 21, 22); 10: Manuripi, Bolivia (Fig. 23); A: Río Tuichi, Bolivia (Wallace *et al.* 2006); B: Río Undumo, Bolivia (Wallace *et al.* 2006); C: Upper Río Madidi, Bolivia (Wallace *et al.* 2006); D: Green Bolivia, Bolivia (Martinez 2010).

The situation around the Los Amigos Biological Station (CICRA) warrants some more attention. Besides the common C. toppini (Fig. 13), there are some reports of darker animals (Figs. 16–17), which could be just a local color variation, as mixed groups are common. Interestingly, of seven pairings studied, all males were dark and the females were distinctly redder (J. Lawrence, pers. comm.). Sexual dichromatism has never been reported in Amazonian Callicebus; extreme intraspecific phenotypic variation is common in C. oenanthe (Proyecto Mono Tocón, unpubl. data), but there is no indication of sexual dichromatism. Martinez and Wallace (2013) reported similar animals from northern Bolivia with dark hands that do not match the holotype of C. toppini. Buchanan-Smith et al. (2002) and Christen (1999) observed titi monkeys in northern Bolivia with very reddish/orange on their backs, while others were medium to dark brown. Callicebus toppini has a grayish to brownish back, but it is difficult to interpret the observations of the animals with the orange backs. It is clear that more research is necessary in this area.

The validity of *C. aureipalatii* remains unclear. The animal that we collected near the Río Urubamba resembles

very much the holotype of *C. aureipalatii* figured in the publication of the original description (Wallace *et al.* 2006). However, *C. aureipalatii* is reported to be different from the animals of Pando, Bolivia (Martinez and Wallace 2013; Porter *et al.* 2013). Molecular genetic investigation is needed to show that this species is not just a color variant of *C. toppini*.

It is interesting to note that a titi monkey from the south bank of the Río Manuripi, Pando, Bolivia, had a karyotype of 2n = 48 (Minezawa *et al.* 1989). It was identified as *C. brunneus*, but as there are only reports of reddish animals from the Pando (Cameron *et al.* 1989; Martinez and Wallace 2013; Porter *et al.* 2013; Erwin van Maanen pers. comm. to JV), the titi in question could have been *C. toppini*. Considering that *C. cupreus* and *C. discolor* (*sensu lato*) have a karyotype of 2n = 46 (Hershkovitz 1990; Bueno *et al.* 2006), this could explain the occurrence of *C. toppini* and *C. discolor* along the Río Ucayali where there is no evidence of a hybrid zone or any geographical barrier. The same is possibly true for *C. toppini* and *C. cupreus* in Peru and Brazil.

In summary, we conclude that the reddish titi monkeys living in south-eastern Peru, south-western Brazil and north-western Bolivia belong to the species *Callicebus toppini*, and we therefore reinstate it. The Río Urubamba seems to be its western geographical barrier. The species is replaced along the Río Ucayali by *C. discolor* and possibly *C. cupreus*, but the exact northern limits are unknown. The eastern barrier is probably the Río Ituxi (where it is parapatric with *C. dubius*), the southern barriers are the Río Tambopata and Río Madre de Dios. If we consider *C. aureipalatii* as a junior synonym of *Callicebus toppini*, its most southerly locality is the Hondo Valley (Martinez and Wallace 2013), while its eastern boundary is the Río Beni (Martinez and Wallace 2013). For convenience, the species have been separated in Figure 24. More research, in the field and in museums, is necessary to determine the exact limits





of the distribution of *C. toppini*. Museum specimens labelled as *C. cupreus* and *C. brunneus* should be re-examined to determine which are actually *C. toppini*.

Callicebus urubambensis sp. nov.

The dark brown specimens labeled as coming from "Mouth Río Inuya, Río Urubamba" and "Boca Río Urubamba", collected by the Olalla brothers and presently in the collection of the American Museum of Natural History, were identified by Hershkovitz (1990) as belonging to *Callicebus brunneus*. However, after observation in the wild, a study of museum specimens and an analysis of the literature, we propose that these animals represent an undescribed species.

Holotype: Adult male, skin and skull. Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42398. Collectors: Jan Vermeer and Julio C. Tello; Proyecto Mono Tocón. Obtained from a hunter on 29 November, 2013, on the left bank of the Río Urubamba (10°48'50"S, 73°17'08"W, altitude 280 m) (Figs. 25–28).

Paratypes: 1) Nulliparous female; skin (forearms missing), skull and complete skeleton. Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima,





Figures 25–28. The holotype of *C. urubambensis* collected on the left bank of the Río Urubamba (specimen deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42398). Photographs by Proyecto Mono Tocón.



Figure 29. The Urubamba brown titi monkey Callicebus urubambensis (left) compared to the, more grizzled, brown titi C. brunneus (right) with a varying amount of black on the head. Illustrations by Stephen D. Nash.

collection no. MUSM 15911. Collected on 12 September, 1999, by B. D. Patterson at Quebrada Aguas Calientes, left bank of the upper Río Madre de Dios, 2.75 km east of Shintuya (71°16'08"W, 12°40'50"S). 2) Subadult male; skin, skull and complete skeleton. Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 15912. Collected on 12 September, 1999, by S. Solari at Quebrada Aguas Calientes, left bank of the upper Río Madre de Dios, 2.75 km east of Shintuya (71°16'08"W, 12°40'50"S).

Type locality: Peru: near the Colonia Penal del Sepa, on the right bank of the Río Sepa, a western tributary of the Río Urubamba (10°48'50"S, 73°17'08"W). Altitude 280 m.

Synonyms: *Callicebus brunneus* in part (Hershkovitz 1963, 1988; Kobayashi 1995; not Wagner 1842).

Diagnostic characters: Forehead with a jet-black band extending to behind the ears. Ears black, covered with long black hairs. Hairs of the cheeks brownish-agouti with long black tips, directed forwards and giving the cheeks, from a

distance, a black color. Chin brown agouti. Facial skin black with black hairs on the cheeks and many white hairs on the nose and around the mouth. Pupils black and irises light brown. Dorsal and lateral side of the body, including the upper arms and the legs, brownish-agouti. Crown the same color as the back. Hands and inner side of the forearms black. Outer side of the forearms black up to the elbow, mixed with a small amount of agouti hairs. Feet black, knees darker than the rest of the leg, giving them a blackish hue. Lateral side of the body, inner side of the upper arms and legs brown-agouti, paler colored than the back. Basal half of the tail almost black, mixed with some brown agouti hairs, becoming lighter towards the end, with a greyish tip.

Paratype 15912 differs in having the forearms less black, with more brown-agouti hairs and a few lighter colored hairs on hands and feet. The same variation is also seen in the six AMNH specimens from the Río Urubamba. We did not observe any variation in the 35 individuals that we



Figure 30. View of the heads of C. urubambensis (left) and C. brunneus (right). Illustration by Stephen D. Nash.





Figures 31 and 32. The lectoparatypes of *C. brunneus* (NMW-ST122 on the left; NMW-B3453 on the right), preserved in the Naturhistorisches Museum in Wien, Austria. The species is more brownish than *C. urubambensis*, has no black forearms and less black around the face. The hairs on the back of the head have yellowish tips. Photographs by Proyecto Mono Tocón.



Figures 33–35. Three *C. urubambensis* from different localities. Individuals shown on the left and in the center: left bank of the Río Urubamba, near the Colonia Penal del Sepa, Peru (Photographs by Proyecto Mono Tocón); specimen on the right: Amazonia Lodge, on the left bank of the upper Río Madre de Dios, Peru (Photograph by Kevin Schafer).

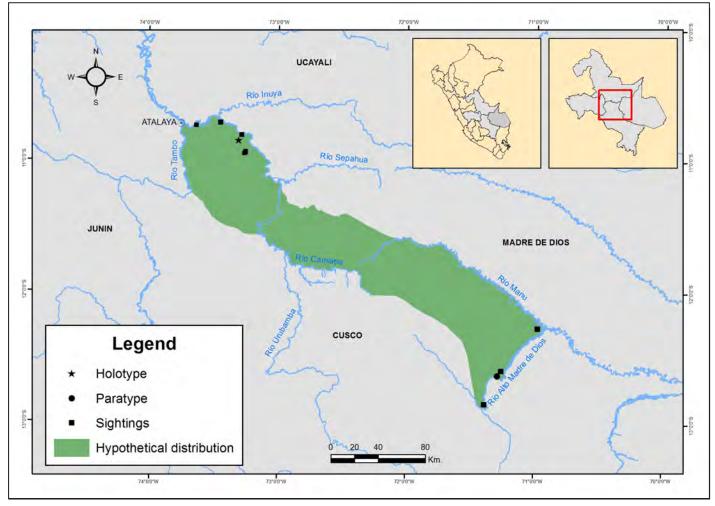


Figure 36. Hypothetical distribution of *Callicebus urubambensis*. Northern sightings during this study, south-eastern sightings along the upper Río Madre de Dios mentioned in the text.

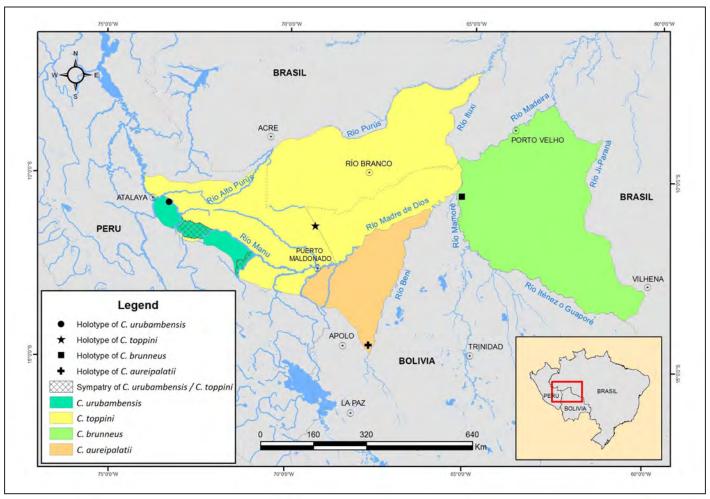


Figure 37. Hypothetical distributions of *Callicebus urubambensis*, *C. toppini*, *C. brunneus*, and *C. aureipalatii*. There is little reliable information on the distribution range of *C. brunneus*; this map is based on Ferrari *et al.* (2000) and Porter *et al.* (2013).

encountered, but it should be noted that it is very difficult to see the details of these dark monkeys in a dark forest.

Comparisons: Distinguished from the partially sympatric *Callicebus toppini* by its dark color and brownish underparts. Along the Río Tambo it is probably allopatric with *Callicebus discolor* from which it is easily distinguished by its black forehead and brown color. It is distinguished from the Brazilian *Callicebus brunneus* (Wagner) by the coloration of the head (Fig. 30). In *C. urubambensis*, the occiput and the sides of the face are the same brown color as the back. In *C. brunneus*, there is a dark brown band behind the jet-black frontal blaze, separating it from the yellowish occiput. The yellowish coloration extends towards the neck, where it becomes the same agouti-brown color as the back and the sides of the body. The cheeks of *C. brunneus* are dark brown, conspicuously darker than the sides of the body.

There is some variation in the coloration of the lecto-(para)-types of *C. brunneus*, but none has the black forearms of *C. urubambensis* (Figs. 31 and 32). There is a geographical gap of more than 600 km between the most eastern observation of *C. urubambensis* and the most western confirmed sighting of *C. brunneus*. Genetic studies could elucidate the taxonomic relationship between the two species.

Measurements of the holotype: Head-and-body length 300 mm; Tail length 400 mm; Foot length 85 mm; Hand length 50 mm; Arm length 120 mm; and Hindleg length 170 mm.

Etymology: This species is named after the Río Urubamba, Peru, where it was discovered.

Vernacular name: The species is locally known as "mono tocón." We propose the name Urubamba brown titi monkey.

Geographical distribution: We encountered C. urubambensis at 12 localities on the left bank of the Río Urubamba. We did not observe it on the right bank of that river or on the left bank of the Río Tambo. The paratypes came from the Quebrada Calientes, on the left bank of the upper Río Madre de Dios, on the eastern border of Manu National Park (71°16'08"W, 12°40'50"S). A photograph of *C. urubambensis* was taken near the Amazonia Lodge, also on the left bank of the upper Río Madre de Dios (71°22'10"W, 12°51'57"S) (Figs. 33-35), while the species was also observed further downriver, near Pantiacolla Lodge (71°14'31"W, 12°39'36"S) and Yine Lodge (approx. 70°55'45"W, 12°16'03"S) (J. Vermeer, pers. obs.). Despite the presence of many researchers and tourists in the Tambopata Nature Reserve and the Los Amigos Biological Station further to the east, there is no evidence that Callicebus urubambensis occurs east of the upper

Table 3. Cranial measurements (mm) of holotype of C. urubambensis MUSM 42398 and paratype MUSM 15912. After Kobayashi (1995).

Cranial measurement	Holotype MUSM 42398	Paratype MUSM 15912
Nasion – Rhinion	9.61	10.42
Rhinion – Prosthion	11.16	8.12
Nasion – Prosthion	20.81	20.43
Left maxillofrontale - Right maxillofrontale	3.59	3.11
Left frontomalare orbitale - Right frontomalare orbitale	28.31	29.59
Left zygomaxillare superior - Right zygomaxillare superior	25.69	26.04
Left frontomalare orbitale - Left zygomaxillare superior	13.12	10.47
Left zygomaxillare superior - Left zygomaxillare inferior	11.70	13.87
Greatest width across outer margins of orbit	33.99	34.00
Left zygion - Right zygion	37.08	37.39
Greatest width across narrowest part in postorbital portion	29.86	29.51
Left euryon - Right euryon	33.97	33.28
Prosthion - Bregma	45.19	45.54
Nasion - Bregma	28.38	27.42
Bregma - Lambda	29.35	29.37
Prosthion - Lambda	58.37	60.45
Basion - Bregma	31.19	32.85
Left zygomaxillare inferior - Right zygomaxillare inferior	30.73	28.34
Left kondilion laterale - Right kondilion laterale	31.38	32.62
Left koronion - Right koronion	34.22	36.27
Infradentale - Left kondilion laterale	37.62	40.98
Infradentale - gnathion	9.84	10.8
Greatest length between left koronion and base of mandibular	31.39	38.34





Figures 38–39. Skull of the holotype of *C. urubambensis* collected on the left bank of the Río Urubamba (specimen deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42398). Photographs by Proyecto Mono Tocón.

Río Madre de Dios, and all available photographs indicate that the titi monkey in those areas is the generally misidentified *C. toppini*.

Although we know that rivers are not absolute geographical barriers for titi monkeys, especially in areas where rivers constantly change their course, we used large rivers to indicate the distributions of the species (Fig. 36). We estimate that the range of Callicebus urubambensis includes the lowland forest area between the right bank of the Río Tambo and the left bank of the Río Urubamba, and the lowland forest between the left bank of the Río Manu and the left bank of the upper Río Madre de Dios. The species' distribution is further restricted by the presence of mountain ridges to the west and south. The situation near the upper Río Urubamba needs further investigation. On both sides of the Río Camisea there are confirmed records only of C. toppini (T. Gregory, pers. comm.). However, somewhere there, there must be a connection between the western and eastern part of the distributions of C. urubambensis, unless in recent history the species has been replaced in that area by C. toppini. The species has been observed to live in sympatry with C. toppini in the eastern part of its distribution, on the left bank of the upper Río Madre de Dios (J. Vermeer, pers. obs.) (Fig. 37).

Systematics: Hershkovitz (1990) and Kobayashi (1995) divided the titi monkeys into species groups. Considering the resemblance in coloration, we would be tempted to place *C. urubambensis* in the same group as *C. brunneus*, which Hershkovitz (1990), Kobayashi, (1995) and Van Roosmalen *et al.* (2002) have in the *moloch* group. Van Roosmalen and Van Roosmalen (2014), on the other hand, placed it in the *cupreus* group. Considering, however, the coloration of neighboring species, we propose that it aligns with the *donacophilus* group (Kobayashi 1995). Following the "metachromism bleaching theory" (Hershkovitz 1988; Van Roosmalen and

Van Roosmalen 2014), *C. urubambensis* would be close to the archetypical taxon of this species group. The dark forehead, forearms, hands and feet show that the species underwent considerable eumelanin saturation, but the process switched to pheomelanin bleaching when members of the species group radiated northwards (*C. oenanthe*, which itself shows pheomelanin bleaching northwards in its restricted range) and south-eastwards (*C. modestus* to *C. olallae* to *C. donacophilus* to *C. pallescens*).

Conservation: The Urubamba brown titi is hunted for food, especially where all the larger primates have been exterminated. As it lives near villages, it is an easy prey for hunters and young boys with slingshots. However, considering its relatively large range with low human presence, there is no immediate threat for this species. It is protected in Manu National Park, and is common along the Río Urubamba (see also Aquino *et al.* 2013).

Callicebus discolor (sensu lato)

We provisionally identify the white-browed titi monkeys along the Río Ucayali as belonging to *Callicebus discolor* (*sensu lato*; but see Vermeer *et al.* 2011 for a discussion on that name) (Figs. 40–42). To be more specific, the animals match closely the *Callicebus subrufus* described by Elliot in 1907. This variation of the white-browed titi monkey is recognized by its rufous back, white ears and the basal half of the tail being black. The hands of many animals are very light colored, but not white. However, similarly colored titis have been reported from Ecuador and it seems that *C. discolor* is a highly variable species, just like *C. oenanthe* (pers. obs.); therefore we should probably list *C. subrufus* as a junior synonym of *C. discolor* (*sensu lato*).







Figures 40–42. Three white-browed titi monkeys, *C. discolor* from different localities. On the left: left bank of the Río Ucayali, Peru (Photograph by Proyecto Mono Tocón); in the middle and on the right: different localities on the right bank of the Río Ucayali, Peru. Photographs by Proyecto Mono Tocón. Notice that the latter animal has a small infant on its flank, possibly only one day old.

According to Hershkovitz (1990), Aquino and Encarnación (1994), and Van Roosmalen *et al.* (2002), *C. discolor* is restricted to the left (western) side of the Río Ucayali. Hershkovitz (1990, p.63) even questions the provenance of two museum specimens in the AMNH (Río Inuya, east bank of the Ucayali) as being "on the wrong side of the Río Ucayali boundary of the *discolor* range." We encountered the species on both sides of the river. This is not surprising, as the Río Ucayali is a river that constantly changes its course. It is possible that on the right bank of the Río Ucayali the white-browed titi is restricted to a narrow strip along the river, and that further inland it is replaced by another species, possibly *C. toppini* or *C. cupreus*. Lacking time, we were unable to determine this.

In order to locate the titis, we often played their vocalization from the Emmons et al. (1998) recordings. According to the authors, the recording we used was of Callicebus moloch brunneus, but considering the taxonomic history described above, this could also be another species. In many cases, individuals of C. toppini and C. urubambensis responded to the recordings. The white-browed titi monkey did not respond. When we recorded their vocalizations and played them to other groups of the same species, they did respond. This could indicate that titi monkeys can distinguish interspecific differences in vocalizations and do not (always) react to the vocalizations of a different species. Such a "linguistic barrier" could prevent interbreeding between different species. It would be interesting to investigate if the differences in vocalizations could be used to identify species or relationships between different species, just as is the case with some other primate species (Zimmermann 2009; Meyer et al. 2012).

Final considerations

To better understand the distributions and taxonomy of titi monkeys in Peru, research should continue further north and eastwards. The northern distributional limit for *C. toppini* and the southern limit for *C. cupreus* need to be established. It would also be interesting to know more about the distribution of *C. discolor* on the right bank of the Río Ucayali. Titi monkeys are often difficult to identify in the forest, especially the darker species, and more museum specimens would help us with understanding the diversity of this genus. Considering the hunting in the region, it should not be difficult for

researchers to obtain skins, skulls and skeletons from local hunters and deposit these materials in museum collections, without promoting (illegal) hunting.

With the addition of these two species, Peru has seven titis; two of them endemic, C. oenanthe and C. urubambensis. The genus Callicebus now comprises 34 species, and, as mentioned, more are likely to be described in the near future. Callicebus, as such, is the primate genus with the most species. As indicated by A. Kitchener (in litt.) reasons for this may be behavioral—small, monogamous groups, in small territories, which limit dispersal—and evidently a result of fluvial dynamics, so marked in the white-water rivers of the western Amazon such as the Ucayali, Amazonas-Marañon, Juruá, and Purús and their tributaries. Hershkovitz (1988) emphasized that changes in the courses of the rivers can isolate small populations or bring together two species previously isolated, resulting in hybridization. The large number of species is of course a consequence of our taxonomy, based almost entirely on morphology, pelage color and patterns, and distributions. Long overdue is a phylogenetic analysis of the genus to elucidate the emergence and composition of the different inferred lineages that are currently expressed only as species groups (Hershkovitz 1990; Kobayashi 1995; Groves 2001). Depending on the phylogenetic history and the ages of the different lineages, it may be appropriate to divide Callicebus into two or more genera, as was resolved recently in the capuchin monkeys (Lynch Alfaro et al. 2012).

Genetic studies of Peruvian primates are hindered by illogical national legislation; it is not difficult to receive a permit to collect dead animal material, but virtually impossible to obtain a permit for materials that will be used for molecular genetic analysis; often the same thing. A better understanding of the taxonomy would help the national government with the development of effective conservation strategies. It is hoped that this frustrating situation will change soon.

Finally, we refer to the discussion (pp.129–130) of the excellent taxonomic revision of the saki monkeys by Marsh (2014). Marsh's observations about the taxonomic confusions permeating *Pithecia* are also relevant for *Callicebus*. Studies on *Callicebus* distributions are confused by erroneous identifications of observed animals. We hope that with our publication we have contributed to a better understanding of titi monkey taxonomy and distribution in Peru. For this study we

received help from people all over the world who provided their photographs for comparison. There are still many gaps in our knowledge of the taxonomy and distribution of titi monkeys in southern Peru and the rest of South America. We call on all researchers, in Peru and other countries, to share their observations and pictures of titi monkeys with us and the *Callicebus* database <www.callicebus.nl>.

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Current Status and Threats to *Lagothrix flavicauda* and Other Primates in Montane Forest of the Región Huánuco

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Abstract: We report on the current status and threats to *Lagothrix flavicauda* and other primates that inhabit montane forest of the Región Huánuco; an area that has been little explored with regard to its primate fauna and other mammals. During 618 km of transect walks in June–July 2014 and September–October 2014, we encountered 47 groups of five primate species, the most common being *Alouatta seniculus* (15 groups) and *Lagothrix flavicauda* (13 groups). We also observed four groups of *Aotus* sp. in the Miraflores census site. *Lagothrix flavicauda* was seen only in the microbasin of the Río Chontayacu, and *Ateles chamek* in the upper Río Huallaga. The primates were living in patches of primary and remnant forest surrounded by farmland and pasture except in Chontayacu, where the forest is still dense and extensive. Of the three species with complete counts, group sizes were largest for *L. flavicauda* (mean 13.6 ± 7.8 , n = 5) and smallest for *A. seniculus* (mean 5 ± 3.5 , n = 11). Population densities were highest for *L. flavicauda* (20.8 ind./km²) and lowest for *Sapajus macrocephalus* (2.7 ind./km²). Deforestation for agriculture and cattle ranching and hunting are the major threats to the survival of these primates. *Sapajus macrocephalus* and *Cebus yuracus* were the most affected by these threats, particularly in the Río Chinchao microbasin,

Key Words: Primates, Andean montane forest, *Lagothrix flavicauda*, threats

Introduction

There are still areas in the Peruvian Amazon where we have little or no information concerning the primate communities occurring there. They are mostly forested areas present in the north and east, near the borders with Ecuador and Brazil, respectively, and premontane and montane forests (500-2800 m) of the Cajamarca, Huánuco, Junín and Ayacucho regions. These regions are remote and difficult to reach, so that information about primates there is scarce and mostly limited to the Peruvian yellow-tailed woolly monkey (Lagothrix flavicauda) and the Andean night monkey (Aotus miconax). Lagothrix flavicauda, one of the world's 25 most endangered primates (Mittermeier et al. 2012), is endemic and lives in cloud forest. There have been some studies of its behavior and feeding (Leo Luna 1980, 1982, 1984; Cornejo 2008), geographical distribution (Shanee et al. 2008; Shanee 2011), and activity budget and behavior patterns (Shanee and Shanee 2011a), but very little is known about the use of forest strata and home range. The presence of L. flavicauda in the premontane and montane forests of the Región Huánuco

was unknown until 2005. Till then it was believed that it was restricted to the cloud forests of the regions of San Martín, La Libertad and Amazonas (Shanee et al. 2008). Aquino (2006) observed a group near the village of Tingo de Uchiza in the Región Huánuco during a wildlife inventory in the Provincia de Tocache, between the Río Chontayacu and the limit with the Provincia de Tocache, Región San Martín. Shanee (2011) considered that its range included the montane forests from the limits of the Provincia de Tocache (Región San Martín) south to probably the Río Magdalena in the Región Huánuco. but Aquino and Ramos (2010) suspected that their distribution would extend further south to include the premontane and montane forests surrounding the ríos Monzon, Patuy Rondos and Chinchao, including Carpish near Tingo María and Pampamarca near the limit with the Región Pasco. For our study area, a few reports indicated the presence of L. flavicauda, the red howler (Alouatta seniculus), and Aotus miconax in premontane forests of the Región Huánuco, but there was no information on their population density, geographic distribution, group size, and food resources and the floristic composition of the forests where they live. The lack of information

regarding these aspects motivated us to carry out this study, the main purpose of which was to determine the current status of *L. flavicauda* and other primates and their habitats, and assess the threats facing the wildlife and the forests there, predictably from agricultural expansion, cattle ranching and floriculture. We hoped to determine the geographic distribution, abundance and population density, and group sizes of *L. flavicauda* and other primates in the south of the Región Huánuco. Here we present the results of a survey conducted between June–July and September–October, 2014, in three sectors of montane forest of the Región Huánuco. The results will be used to recommend areas for the conservation of primates and other wildlife, and to promote environmental education, especially in the villages surrounding the study area.

Methods

Study area

The Región Huánuco is in central Peruvian Amazonia. The forests of this region, including the premontane and montane forest, are being cut down for agriculture, timber extraction, cattle ranching and floriculture. There is some subsistence hunting, and monkeys, particularly *Cebus yuracus* and *Sapajus macrocephalus*, are shot as crop-raiders, when they enter maize plantations to eat the unripe corn called "choclo." We identified three sectors for the surveys, each with two census sites (Fig. 1). Table 1 gives their geographic coordinates and elevation, and indicates the extent of human disturbance. The sampling sectors were as follows.

The microbasin of the Río Chontayacu, including the forest of the Río Bardales near the village of Cocalito on the left bank, and the Río Yanajanca on the right bank. At both census sites the forests were moderately disturbed, mainly due to timber extraction and subsistence hunting. Deforestation for agriculture is increasing with the construction of the Uchiza-Huacrachuco road.

The microbasin of the Río Chinchao, including the forests of the villages of San Pedro de Carpish and Ñaupamarca, on each bank of the Río Chinchao. This sector is dominated by remnant forest patches, and is being deforested for agriculture and floriculture.

The upper basin of the Río Huallaga, on the right bank; the forests surrounding the villages of Miraflores and Santa Ana. The forests along both sides of the Río Alto Huallaga are extensively deforested for cattle ranching and the construction of a hydroelectric dam.

Transect censuses

For transect censuses we used the paths and trails of the loggers, farmers and hunters. Each transect was walked two or three times. The censuses were conducted from 07:00 to 16:00 h. Two teams of two observers walked simultaneously along two different transects, with an average speed of 0.5 km/h. Each time a primate group was detected, the recorded the following information: group size (when possible); perpendicular distance from the transect of the first individual seen; height (in the forest stratum); activity at the moment of detection; presence of juveniles and infants; and vegetation type. Censuses were conducted on the transects in both directions (inbound and outbound). Taking into account the physiographic characteristics of the montane forest, we walked 618 km-267 km in the microbasin of the Río Chontayacu, 131 km in the microbasin of the Río Chinchao, and 220 km in the upper basin of the Río Huallaga; equivalent to 876 census hours (Table 2).

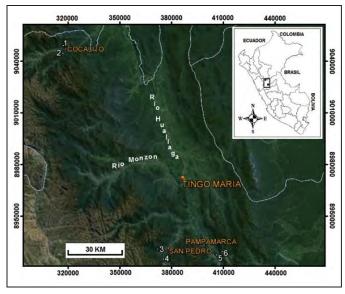


Figure 1. Location of sampling sectors and census sites in the montane forest of the Región Huánuco. Río Chontayacu microbasin (sites 1 and 2), Río Chinchao microbasin (sites 3 and 4), and Río Alto Huallaga (sites 5 and 6).

Table 1. Census sites in the montane forest of the Región Huánuco.

Sampling sectors	Census sites*	Coordinates (UTM)	Altitude (m.a.s.l.)	Degree of human disturbance
Río Chontayacu microbasin	Bardales (1)	320373/9048536	1495	Moderate
	Yanajanca (2)	317857/9042750	1620	Moderate
Río Chinchao microbasin	Ñaupamarca (3)	379516/8930750	1883	Very high
	Carpish (4)	381695/8929094	2418	Very high
Río Alto Huallaga	Miraflores (5)	510182/8929316	1862	High
	Santa Ana (6)	413452/8929274	1496	High

^{*}Numbers in parenthesis correspond to the points in Figure 1.

Floristic composition of the montane forests

In the Chontavacu sector, we demarcated a strip of 20×1 m (coordinates: 315472/9048057; elevation: 1480 m) and a plot of 50×10 m (coordinates: 331061/9051625; elevation: 1051 m). In the Chinchao sector we demarcated two strips, one of 50×1 m (coordinates: 381376/8929884; elevation: 2369 m) and the other of 30×1 m (coordinates: 381287/8930057; elevation: 2231 m). The botanical samples were prepared for the herbarium following the methodology of Judd et al. (1999). They were identified in the Herbario Amazonense (AMAZ) of the Universidad Nacional de la Amazonía Peruana and Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos, with the help of the keys of Spichiger et al. (1989, 1990), Gentry (1993), Vásquez (1997), Ribeiro et al.(1999), and others. The botanical specimens were deposited in the herbarium of the Instituto de Investigaciones de la Amazonía Peruana (IIAP).

Data analysis

Group size was determined on fully counted groups, excluding dependent infants. Each time we contacted the primates, we counted the number of individuals and, when possible, also the adults (males and females), juveniles and infants. Due to the small number of sightings (<30) for *L. flavicauda* and other species, we used the formula suggested by Burnham *et al.* (1980) for calculation of densities: D = N / 2dL, where D is the density (groups/km²), N the number of sightings, L the accumulated transect length, and d the mean perpendicular distance to the transect. Except for *C. yuracus* and *S. macrocephalus*, the population density was then obtained by multiplying D by mean group size. For *C. yuracus* and *S. macrocephalus*, we considered the highest group sizes counted, which were 11 and 9, respectively. To obtain relative abundances, we calculated the number of sightings per

10 km of transect walked. Sightings and density calculations for *A. seniculus*, *C. yuracus* and *S. macrocephalus* are based on the total 618 km of transect. Calculation for *L. flavicauda* and *A. chamek*; are based on 267 km and 220 km, respectively, because *L. flavicauda* does not occur in the forest of the upper Río Huallaga, and was not confirmed to occur in Capish and Ñaupamarca (sector of the Río Chinchao microbasin), while *A. chamek* apparently does not occur in the microbasins of Chontayacu and Chinchao. Why these species are absent from these areas is unknown.

Results

Forty-seven groups of five primate species were observed during the survey. We also encountered four groups of *Aotus* sp. (probably a new species) in forests surrounding the village of Miraflores, on the right bank of the Rio Huallaga when we were not surveying. The range of this species probably extends south to the montane forests of the Región Pasco. Most commonly seen were *A. seniculus* (n = 15) and *L. flavicauda* (n = 13); the fewest sightings were of the tufted capuchin *S. macrocephalus* (Table 3).

Of the five species recorded during the census, *L. flavicauda* (Fig. 2) was observed only in the Bardales and Yanajanca sites around the village of Cocalito in the Río Chontayacu microbasin, and *A. chamek* (Fig. 3) was seen only in Miraflores and Santa Ana sites located in the upper Río Huallaga basin. *Alouatta seniculus* was the only species observed in all census sites. *Cebus yuracus* and *S. macrocephalus* were not observed in Carpish and Ñaupamarca (Sector Chinchao), although people affirmed that both occur there and are pests raiding corn and other crops. They also told us that *L. flavicauda* occurs in this sector and is seen most frequently from December to February, coinciding with the production

Table 2. Distance traveled and census hours by census site in the sampling sectors.

Sampling sectors	Census sites	Transect length (km)	Effort – time censused (hours)	
Río Chontayacu microbasin	Bardales	116	179	
	Yanajanca	151	231	
Río Chinchao microbasin	Ñaupamarca	62	87	
	Carpish	69	107	
Río Alto Huallaga	Miraflores	151	185	
	Santa Ana	69	87	
Total		618	876	

Table 3. Primate species and numbers of groups registered in the sampling sectors.

		T. 4. 1			
Species	Chontayacu	Chinchao	Alto Huallaga	Total	
Lagothrix flavicauda	13			13	
Ateles chamek			8	8	
Alouatta seniculus	6	5	4	15	
Sapajus macrocephalus	2		3	5	
Cebus yuracus	4		2	6	
Total	25	5	17	47	

of wild fruits, particularly *Cecropia* sp. "tacones." People at Carpish described it accurately and a short expedition should be carried out to confirm or discard this possibility. For now we consider the Río Alto Huallaga as the limit of their geographic distribution southward, but it will be important still to

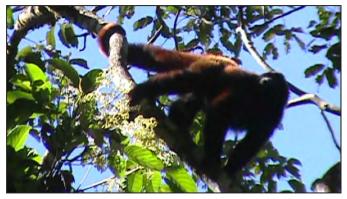


Figure 2. Adult Peruvian yellow-tailed woolly monkey (*Lagothrix flavicauda*) in the Yanajanca census site, sector Chontayacu.



Figure 3. Adult black-faced black spider monkey *Ateles chamek* in Santa Ana, Sector Río Alto Huallaga.

explore the microbasins of the ríos Magdalena and Monzón to confirm or discard the presence of this species in this part of the Región Huánuco.

With regard to *L. flavicauda*, eight of the 13 registered groups were observed in the Yanajanca forest (right bank of Río Chontayacu), the others in the Bardales forests on the left bank of this river near to the village of Cocalito (Table 4). In Yanajanca, we also saw an adult female, who we followed for two hours hoping to find the other members of her group. She did not contact a group during this time, however, so she may have been dispersing. She did not show any behavior indicating she was lost; on the contrary, she just foraged and rested. We observed others groups at elevations of 1572 m to 2045 m along with *A. seniculus*, *S. macrocephalus* and *C. yuracus*.

Dependent infants were observed in some groups of the five recorded species. There were one to four infants in most of the *L. flavicauda* groups (Table 4). Infants were on the mother's back, except in two cases where they were nestled between the mother's neck and chest. This would indicate that the reproductive season of *L. flavicauda* and the other primates that inhabit these montane forests would be from January to April. Juveniles observed would correspond to births of the previous year.

Alouatta seniculus was the only species registered in Carpish, in the Río Chinchao microbasin. Groups were seen in patches of primary and residual forests there. In Miraflores and Santa Ana (Río Alto Huallaga), the primates were inhabiting patches of primary forest on the steep and rugged slopes. In Yanajanca and Bardales (Río Chontayacu), however, *L. flavicauda* and other primates were found in relatively dense and extensive primary forests.

The variation in group size in the three species with complete counts is similar to those recorded for these species in other parts of the Peruvian Amazon with physiography varying from montane (*L. flavicauda*) to sub-montane (*A. chamek* and *A. seniculus*) (Table 5). We were unable to determine

Table 4. Groups of Lagothrix flavicauda observed in the Río Chontayacu microbasin.

Groups	Size	Census sites	River bank	Coordinates (UTM)	Altitude (m.a.s.l.)	Observations
1	>3	Yanajanca	Right	317853/9042935	1572	
2	6	Yanajanca	Right	317966/9043238	1682	+1 infant
3	>12	Yanajanca	Right	318004/9043342	1705	+2 infants
4	>8	Yanajanca	Right	317850/9042934	1575	+1 infant
5	13	Yanajanca	Right	317951/9043170	1661	+2 infants
6	>8	Yanajanca	Right	317852/9042932	1572	+1 infant
7	23	Yanajanca	Right	317874/9042994	1579	+4 infants
8	6	Yanajanca	Right	317176/9043791	2045	
9	>6	Bardales	Left	320302/9048832	1673	
10	>7	Bardales	Left	320993/9048710	1823	
11	20	Bardales	Left	321174/9048894	1760	+3 infants
12	>1	Bardales	Left	321265/9049032	1781	
13	>5	Bardales	Left	321268/9049036	1783	+2 infants

the average group size for *C. yuracus* and *S. macrocephalus* because they were so skittish, persecuted as they are for their crop raiding. The primates in Bardales, near to the village of Cocalito, suffer from subsistence hunting. In forests near the road (2 to 3 km), groups of *L. flavicauda* and *A. seniculus* were small and fearful. In more distant forests (3 km or more from the road), groups were larger and easier to observe. In Yanajanca, all groups seen were quite tame and tolerant of humans watching them. Dependent infants were not considered in the group-size count, but as many as three infants were observed in some *L. flavicauda* groups there. The number of sightings and the population densities were higher for *L. flavicauda* and *A. chamek*, than for the other species, notably *S. macrocephalus* with only 0.08 groups/10 km and 2.7 indiv./ km² (Table 6).

In the microbasin of the Río Chontayacu, between Cocalito and San Antonio de Padua, the floristic composition was composed of trees of 18-25 m height, with some emergents up to 30 m, and with trunk diameters at breast height largely in the classes of 10 to \leq 20 m (36.7 %) and 20 to \leq 30 m (5.0 %). There, the most representative life forms were trees and shrubs, along with epiphytic plants, mainly mosses, on the stems. We recorded 75 species (Table 7); of which, Pseudolmedia macrophylla (Moraceae), Himatanthus sucuuba (Apocynaceae) and *Nealchornea yapurensis* (Euphorbiaceae) were the most representative of the middle stratum and canopy, while the understorey was populated mainly by Cyathea sp. (Cyatheaceae). Notable among the epiphytes and hemiepiphytes were Lomariopsis latipinna (Lomariopsidaceae) and Columnea sp. (Gesneriaceae), and among the lianas Arrabidaea sp. (Bignoniaceae) and Ficus pertusa (Moraceae).

In Carpish, the vegetation was composed of trees 15 m tall, with some emergents up to 20 m. Trunks and branches were laden with epiphytes. In contrast to Chontayacu, we recorded only 35 species, indicating the extent of disturbance in these forests (Table 7). Ferreyranthus excelsus (Asteraceae), Cavendishia punctata (Ericaceae) and Podocarpus oleifolius (Podocarpaceae) are among the most representative species of the middle stratum and canopy, while in the understorey there are many Baccharis sp. (Asteraceae), Diplazium sp. (Dryopteridaceae), Gaultheria sp. (Ericaceae) and Miconia sp. (Melastomataceae). Among the epiphytes and hemiepiphytes were Stenospermation killipii (Araceae), Pitcairnia sp., Tillandsia sp. (Bromeliaceae) and Epidendrum sp. (Orchidaceae), and among lianas and climbing plants Clusia minor, Clusia sp. 1 (Clusiaceae), Dioscorea sp. (Dioscoreaceae) and Manettia sp. (Rubiaceae).

Deforestation is the main threat to the survival of primates and other wildlife in the areas we surveyed. The forest is cut for agriculture and cattle ranching, most extensively in the Alto Huallaga and Chinchao sectors (Figs. 4 and 5), currently less so in Chontayacu, but deforestation will undoubtedly increase in the near future with the improvement of the Uchiza-Huacrachuco road. Deforestation is also related to illegal commercial logging in the microbasin of the Río Chontayacu (Fig. 6). Forest burning is another threat. Fires are used by the Andean people to improve the quality of the pasture and soil, and to reduce costs in the maintenance of good pasture for the cattle. Wildfires affect not only the shrubby thickets and pasture, but also the primary forest.

In the study area there are two types of hunting: (1) to reduce crop raiding and (2) for subsistence. People shoot

Table 5. Group sizes of primates encountered during transect surveys.

	Group	p size	Number	of groups		
Species	Mean ±SD	Range	Total	With complete group count	Group size range in other areas	
Lagothrix flavicauda	13.6 ±7.8	6-23	13	5	3-19 ^a	
Ateles chamek	10 ±6.2	3-15	8	2	8-17 ^b	
Alouatta seniculus	5 ±1.9	3-9	15	11	4-8 ^b	
Sapajus macrocephalus		>11	5		7-11 ^b	
Cebus yuracus		>9	6		6-13 ^b	

^a La Esperanza: Shanee and Shanee (2011).

 Table 6. Sightings rates and population density estimates for the study area.

	Mean detection	Total length of	# of sightings/10 km	Population density		
Species	distance [m] transect walks [km]		of transect walk	Groups/km ²	Ind./km ²	
Lagothrix flavicauda	16	267	0.5	1.53	20.8	
Ateles chamek	12	220	0.36	1.5	13.5	
Alouatta seniculus	12	618	0.24	1	5	
Sapajus macrocephalus	14	618	0.08	0.3	3.3	
Cebus yuracus	10	618	0.1	0.5	4.5	

^b Urubamba and Tambo: Aquino et al. (2013).

 Table 7. Floristic composition of Chontayacu and San Pedro de Carpish montane forest.

Family	Species	Habit*	Montane forest (ind./plot)		
	_		Chontayacu	San Pedro de Carpis	
Anacardiaceae	Astronium sp. 1	T	1		
	Mauria ferruginea	Т		1	
	Tapirira guianensis	T	1		
Apocynaceae	Himatanthus sucuuba	T	3		
Araceae	Monstera sp. 1	Н Не	1		
	Philodendron sp. 1	Н Не	1		
	Philodendron sp. 2	Н Не	1		
	Stenospermation amomifolium	Н Не	1		
	Stenospermation killipii	Н Не		1	
Arecaceae	Ceroxylon sp. 1	De	1		
Araliaceae	Oreopanax sp. 1	Sh		1	
Asteraceae	Ageratina sp. 1	Sh		1	
	Baccharis sp. 1	Sh	1	2	
	Baccharis trinervis	Sh		1	
	Chromolaena laevigata	Sh	1		
	Ferreyranthus excelsus	Sh		4	
	Munnozia hastifolia	Sh	2		
	Schistocarpha eupatorioides	Н		1	
	Vernonanthura patens	Sh	2		
	Vernonia sp. 1	Sh	1		
Begoniaceae	Begonia bracteosa	Н		1	
	Begonia parviflora	Sh		1	
	Arrabidaea sp. 1	L	1		
Bromeliaceae	Guzmania sp. 1	Н Ер	1		
	Pitcairnia sp. 1	Н Ер		2	
	Tillandsia sp. 1	Н Ер		1	
Burseraceae	Dacryodes sp. 1	T	1		
	Protium altsonii	T	1		
	Tetragastris panamensis	T	2		
Cecropiaceae	Cecropia sciadophylla	T	1		
-	Coussapoa sp. 1	T	1		
	Pourouma bicolor	T	1		
Chloranthaceae	Hedyosmum sp. 1	Sh	1	1	
Chrysobalanaceae	Licania sp. 1	T	1	-	
Clusiaceae	Chrysochlamys ulei	T	1		
	Clusia minor	L	1	1	
	Clusia sp. 1	L		1	
		Sh	1	1	
Commelinaceae	Marila sp. 1 Dichorisandra ulei	- Sn H	1		
Cyatheaceae					
Cyclanthaceae	Cyathea sp. 1	De	3		
Сустанинассас	Asplundia sp. 1	Н Не	1		
Cymaragaga	Cyclanthus bipartitus	Н	1		
Cyperaceae	Oxycaryum cubense	Н	1		

table continued on next page

Table 7. continued

Family	Species	Habit*	Montane forest (ind./plot)		
	aprilia .		Chontayacu	San Pedro de Carpis	
Dryopteridaceae	Cyclodium meniscioides	Н Ер	1		
	Diplazium sp. 1	Н		2	
Ericaceae	Cavendishia punctata	Sh		3	
	Gaultheria sp. 1	Sh		2	
Euphorbiaceae	Croton sp. 1	T	1		
	Hevea guianensis	T	1		
	Hyeronima oblonga	T	1		
	Mabea occidentalis	T	2		
	Nealchornea yapurensis	T	3		
	Sapium glandulosum	T	1		
Fabaceae	Dussia sp. 1	T	1		
Flacourtiaceae	Casearia arborea	Sh	1		
	Casearia commersoniana	Sh	2		
Gesneriaceae	Columnea sp. 1	Н Ер	2		
Lauraceae	Nectandra sp. 1	T		1	
	Nectandra sp. 2	T		1	
	Pleurothyrium sp. 1	T	1		
Lecythidaceae	Eschweilera bracteosa	T	1		
Liliaceae	Bomarea sp. 1	Н		1	
Lomariopsidaceae	Elaphoglossum sp. 1	Н		1	
	Lomariopsis latipinna	Н Не	2		
Marantaceae	Ischnosiphon gracilis	Н	1		
	Monotagma juruanum	Н	1		
Melastomataceae	Aciotis sp. 1	Sh		1	
	Miconia sp. 1	Н	1		
	Miconia sp. 2	Н		2	
	Miconia sp. 3	Н		2	
	Tibouchina longifolia	Sh	1		
	Tibouchina sp. 1	Sh		1	
Moraceae	Batocarpus orinocensis	T	1		
	Brosimum lactescens	T	1		
	Clarisia racemosa	T	1		
	Ficus pertusa	L He	1		
	Pseudolmedia laevigata	T	1		
	Pseudolmedia macrophylla	T	5		
Myricaceae	Morella pubescens	Lt		1	
Myristicaceae	Virola sp. 1	T	1		
Myrsinaceae	Cybianthus sp. 1	Sh		1	
	Myrsine manglilla cf.	Sh	2		
Myrtaceae	Calyptranthes sp. 1	Sh	1		
	Myrcia fallax	Sh	1		
Nyctaginaceae	Neea divaricata	Sh	1		
Olacaceae	Minquartia guianensis	T	1		
Orchidaceae	Epidendrum sp. 1	Н Ер		1	

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Table 7. continued

E9	Species	Habit*	Montane forest (ind./plot)		
Family	Species	Habit^	Chontayacu	San Pedro de Carpish	
Piperaceae	Peperomia sp. 1	Н Ер		1	
	Piper sp. 1	Sh		1	
	Piper sp. 2	Sh	1		
Podocarpaceae	Podocarpus oleifolius	T		2	
Polygonaceae	Triplaris setosa	Lt	1		
Polypodiaceae	Campyloneurum sp. 1	Н	1		
Rubiaceae	Elaeagia sp. 1	T	1		
	Faramea sp. 1	Lt		1	
	Ladenbergia oblongifolia	T	1		
	Manettia sp. 1	L		1	
	Psychotria buchtienii	Sh	1		
Sapotaceae	Chrysophyllum sp. 1	T	2		
	Pouteria ambelaniifolia	T	1		
	Pouteria torta	T	1		
Selaginellaceae	Selaginella geniculata	Н	1		
	Selaginella haematodes	Н	1		
Solanaceae	Trianaea sp. 1	Sh		1	
Sterculiaceae	Theobroma subincanum	T	1		
Violaceae	Leonia glycycarpa	T	2		
	Leonia sp. 1	T	1		
Vochysiaceae	Qualea paraensis	T	1		
	Vochysia sp. 1	T	1		

^{*}T = Tree; Sh = Shrub; De = Dendriform (basal branching); S = Suffrutescent (somewhat shrubby, or shrubby at the base); H = Herb; L = Liana, Cp = Climbing plant; Lt = Small tree; H Ep. = Epiphyte herb; H He = Hemiepiphyte herb; and L He = Hemiepiphyte liana.



Figure 4. Deforestation for cattle pasture in the Santa Ana census site, sector Alto Huallaga.



Figure 5. Deforestation for agricultural land in Carpish census site, sector Chinchao.



Figure 6. Illegal logging in Cocalito near the Bardales census site, Sector Chontayacu.

capuchin monkeys, *S. macrocephalus* and *C. yuracus*, because of their crop raiding in Chinchao and Alto Huallaga. Only subsistence hunting was recorded in the Río Chontayacu microbasin, occupied by transients and loggers.

Discussion

The diversity of primates recorded in the Miraflores and Santa Ana montane forests in the Río Alto Huallaga was much higher than in the other census sites, including the premontane and montane forests of the San Martín, Huánuco, and Amazonas regions surveyed by Shanee *et al.* (2013). We observed *S. macrocephalus* and *C. yuracus* at elevations of 1600–1880 m, and Butchart *et al.* (1995) found *S. macrocephalus* in the Cordillera de Colán at 2350 m; records above the maximum elevation indicated by Emmons and Feer (1990) for this species (to 1500 m).

According to Shanee (2011) the southern limit of the range of *L. flavicauda* in Huánuco would probably be the Santa Martha or Magdalena river valleys or the intervening highlands. We suspect that their distribution could reach up to the premontane and montane forests of the left bank of the upper basin of the Río Huallaga. Their absence during our surveys in Carpish and Ñaupamarca does not rule out this possibility; first, because the descriptions of the pelage by two people interviewed in Carpish coincide clearly with the phenotypic characteristics of this primate, and second, because in the past there was no geographical or ecological barriers that might prevent their occurrence between the upper basin of the Río Huallaga and the Río Chontayacu.

In Carpish and Naupamarca, *A. seniculus* was found inhabiting patches of primary forest present on the rugged hillsides, where agriculture or cattle ranching are impossible, and in remnant forest patches, degraded by the extraction of timber trees. These patches are isolated by fields and pasture, which the howlers have to cross when moving from one patch to another, exposing themselves to dogs and wild carnivores

such as the tayra (Eira barbara), which is common in high forest and cloud forest. In Miraflores and Santa Ana, the primary forest is much more extensive compared to Naupamarca and Carpish, where the forests are more patchy and isolated, separated by large expanses of open pasture, probably limiting the movements of primates, particularly during the summer when the insolation is intense in the open fields. Although for now our perception is that the primates are doing well in these primary forest patches, the medium-term prospects are not good, with the inevitable erosion of forest cover due to the burning practiced by the settlers, whose justification is the need to improve pasture quality and to lower costs in the maintenance and expansion of pasture for their cattle. In Bardales and Yanajanca in the Río Chontayacu microbasin, primary forest is continuous and present on both sides of the river from Cocalito downstream to San Antonio de Padua, where L. flavicauda and other primates were most abundant. Until the end of 2012, deforestation in this part of Chontayacu did not surpass one kilometer from the river edge, but with the building of the Uchiza-Huacrachuco road deforestation is increasing due to logging for valuable hardwoods and expanding agriculture and cattle ranching. Prospects for the future are not good, and the creation of a conservation area and, simultaneously, the promotion of ecotourism to benefit local communities, is essential to protect this significant population of L. flavicauda.

Group sizes (range and mean) of *L. flavicauda* recorded in this study are similar to those obtained for La Esperanza (Shanee and Shanee 2011b) and the Río Abiseo National Park (Leo Luna 1982). Group sizes were smaller than those reported for the Bosque de Protección Alto Mayo, where the groups were relatively large (17 to 20 individuals) (DeLuycker 2007), but larger than those obtained for the Area de Conservación Privada Abra Patricia – Alto Nieva (average 5.53 individuals; range 2–7) (Cornejo 2007). Group sizes of other species, particularly of *A. chamek* and *A. seniculus*, were very close to those reported for the Río Urubamba – Río Tambo interfluvium, particularly those recorded in premontane forest (Aquino *et al.* 2013).

The population density of L. flavicauda estimated in the Chontayacu sector was very similar to that reported by Leo Luna (1982, 1987) for the Río Abiseo National Park, who used the traditional method of line transect surveys, and also similar to the density found by Shanee and Shanee (2011a) at La Esperanza. It was higher than the density estimated for the Area de Conservación Privada Abra Patricia - Alto Nieva (Cornejo 2007), which would indicate that in Chontayacu populations of L. flavicauda are still healthy. In the case of A. chamek, population density was higher than that reported for the interfluvium of the ríos Urubamba and Tambo, where montane forest is predominant (Aquino et al. 2013). In this regard, Shanee (2009) concluded that spider monkey densities tend to drop with increasing elevation, but our results indicate the opposite. These populations are not hunted, and it is possible that the higher population density in Huánuco comes from crowding in the forest patches.

The Andean people in these regions are farmers and cattle ranchers and, except for *S. macrocephalus* and *C. yuracus*, in general the primates are not heavily hunted. This could explain the large groups, and shows that these primates can survive in disturbed habitats when there is little hunting. The most critical problem is the forest loss occasioned by deforestation, most intense in the Chinchao sector, where the red howler groups live in small patches of remaining forest, while in other sectors there is still primary forest, particularly in the basins of the ríos Yanajanca and Bardales in the Chontayacu sector, which must be evaluated as ideal for the creation of a conservation area and an ecotourism business to ensure the survival of *L. flavicauda* and its forests.

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A New Species in the Genus *Cheirogaleus* (Cheirogaleidae)

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Abstract: The genus *Cheirogaleus*, the dwarf lemurs (Infraorder Lemuriformes), has been identified as harboring cryptic species diversity. More comprehensive fieldwork combined with improvements in genetic research has revealed a larger radiation of species than was initially described in a number of lemur genera, including *Avahi*, *Lepilemur*, *Microcebus*, and *Mirza*. Available genetic and morphological evidence suggests that *Cheirogaleus* is among the genera where diversity was previously underestimated, and additional fieldwork may reveal even more species. A population of *Cheirogaleus* from northern Madagascar in and around Montagne d'Ambre National Park, surveyed during an expedition in 2005, was recently identified and proposed as a new species. Additional specimens were obtained during fieldwork in February of 2015. Subsequent genetic and morphological analyses of the data collected have determined that this population is an independent lineage, and herein we describe this new species, which we name *Cheirogaleus andysabini* after New York philanthropist Andy Sabin.

Key Words: Cheirogaleus, cryptic species, dwarf lemurs, Madagascar, new species

Introduction

The dwarf lemurs (genus *Cheirogaleus*) are a radiation of small, arboreal primates endemic to the island of Madagascar (Mittermeier *et al.* 2010). The taxonomy and species status in *Cheirogaleus* has been contentious; a situation exacerbated by the limited number of specimens available for study in collections (Schwarz 1931; Groves 2000; Lei *et al.* 2014). Groves (2000) recognized seven *Cheirogaleus* species (*C. major*, *C. medius*, *C. crossleyi*, *C. adipicaudatus*, *C. sibreei*, *C. ravus*, and *C. minusculus*); a number that has been challenged as overly conservative in recent fieldwork and genetic analyses, suggesting a larger radiation in this genus (Hapke *et al.* 2005; Groeneveld *et al.* 2009, 2010; Thiele *et al.* 2013; Lei *et al.* 2014).

Concerns about overenthusiastic species descriptions in the lemuriform radiation raised by Tattersall (2007, 2013) have been addressed previously in Lei *et al.* (2014). Application of the Phylogenetic Species Concept and access to data from molecular technology (Eldredge and Cracraft 1980; Wheeler and Platnick 2000) has nearly tripled the number of recognized lemur species since the early 1980s (36 to >103; Tattersall 1982; Mittermeier *et al.* 2010). *Cheirogaleus* has not experienced the type of genus-level expansion seen in

Lepilemur (Louis et al. 2006) or Microcebus (Mittermeier et al. 2010); genera with the greatest increases in recognized species diversity. Nevertheless, Cheirogaleus appears to be harboring greater diversity than previously suspected (Thiele et al. 2013; Lei et al. 2014).

A new species of Cheirogaleus was identified via extensive fieldwork in and around Montagne d'Ambre National Park (Fig. 1) in November of 2005 (Lei et al. 2014), with additional fieldwork in February of 2015. The massif of Montagne d'Ambre is of volcanic origin (Segalen 1956), and this rain forest ecotype may have been separated from the surrounding dry deciduous vegetation for millions of years (Raxworthy and Nussbaum 1994), with the last volcanic eruptions occurring as recently as 2 mya (DuPuy and Moat 1996). It has a distinctive microclimate that is in part the result of greater than average precipitation in comparison to the surrounding areas. Raxworthy and Nussbaum (1994) noted the presence of species there that were altitudinal specialists, with those above 900 m living in moist rainforest, and those below 900 m living in a transitional area with a dry deciduous forest. Montagne d'Ambre's combination of geology and climate has resulted in a unique community of microendemic fauna and flora; plants (Mathieu 2003; Callmander et

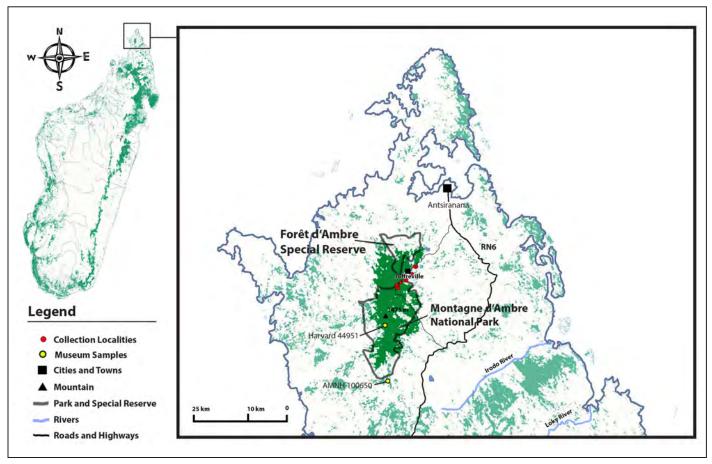


Figure 1. Map of Montagne d'Ambre and the surrounding region in northern Madagascar. Red circles in and around Montagne d'Ambre represent collection localities of *Cheirogaleus* sp. nov. 1 individuals listed in Tables 1 and 2. Yellow circles represent two museum samples, Harvard Museum of Comparative Zoology (MCZH) 44951 received in January 1929 as part of the Grandidier collection and American Museum of Natural History (AMNH) 100650 collected November 7, 1930 by Austin L. Rand, that are holotype candidates (The MCZH 44951 is missing in inventory, 1994.).

al. 2009), amphibians (D'Cruze et al. 2010; Rakotoarison et al. 2015), reptiles (Raxworthy and Nussbaum 1994; D'Cruze et al. 2008; Glaw et al. 2009; Ratsoavina et al. 2011), birds (Wilmé 1996), and mammals (Louis et al. 2008; Goodman et al. 2015).

The first herpetological survey in the area of Montagne d'Ambre was carried out in 1893, and subsequent expeditions have cataloged the regional endemism of the park and surrounding area (D'Cruze at al. 2008). The national park and surrounding region continues to be an exciting source of new species, including a chameleon in the genus Furcifer (Glaw et al. 2009). The area is also home to a number of lemurs, including two species in the genus Eulemur (E. coronatus and E. sanfordi), the Montagne d'Ambre fork-marked lemur (Phaner electromontis), the aye-aye (Daubentonia madagascariensis), and the recently described Montagne d'Ambre mouse lemur (Microcebus arnholdi Louis et al., 2008). Malagasy endemic carnivores are also found in the park, including the rare falanouc (Eupleres goudotii) and the ring-tailed mongoose (Galidia elegans) (Mittermeier et al. 2010).

The area around Montagne d'Ambre National Park and the Forêt d'Ambre Special Reserve were initially protected in the 1920's as a forest station called 'Les Roussettes'. In 1958, Montagne d'Ambre became the first national park created in Madagascar, and the Forêt d'Ambre S.R. was created the same year (Raxworthy and Nussbaum 1994). Subsequent deforestation has reduced the size of both the national park and the special reserve, in particular impacting the lowland rainforests (those below 900 m). More than twenty years ago, Raxworthy and Nussbaum (1994) observed a noticeable difference in forest cover based on a comparison of aerial photographs from the 1950s and the early 1990s. Ongoing deforestation has since been noted by Glaw and Vences (2007) and D'Cruze *et al.* (2008), among others.

Montagne d'Ambre National Park, like much of the remaining forested areas of Madagascar, is under the greatest threat from a combination of slash-and-burn agriculture (tavy) and charcoal extraction (Nicoll and Langrand 1989). The growth of the nearby port city of Antsiranana (formerly Diego Suarez) has accelerated deforestation by greatly increasing the demand for charcoal, a primary source of fuel for cooking. The town of Joffreville, named for the French General Joseph Joffre of First World War fame and located just east of the national park, is a center of charcoal extraction. As of 2001, 98% of the population of Joffreville was employed primarily in agriculture, with 90% farming and 8%

Table 1. Free-ranging *Cheirogaleus* samples used in this study. IDs correspond to Figure 2 and Figure 5 (Lei *et al.* 2014), with the exception of the samples from Thiele *et al.* 2013 (denoted at the bottom of the table, as well as on the map).

ID	Species designation	Location	Latitude	Longitude
AMB5.22	C. sp. nov. 1	Montagne d'Ambre	-12.52731	49.17331
AMB5.23	C. sp. nov. 1	Montagne d'Ambre	-12.53017	49.17464
AMB5.27	C. sp. nov. 1	Montagne d'Ambre	-12.51722	49.1795
AMB5.28	C. sp. nov. 1	Montagne d'Ambre	-12.47881	49.21222
AMB5.29	C. sp. nov. 1	Montagne d'Ambre	-12.47922	49.21606
AMB5.30	C. sp. nov. 1	Montagne d'Ambre	-12.47917	49.21597
AMB5.31	C. sp. nov. 1	Montagne d'Ambre	-12.51083	49.19275
AMB5.32	C. sp. nov. 1	Montagne d'Ambre	-12.51242	49.18956
AMB5.34	C. sp. nov. 1	Montagne d'Ambre	-12.47822	49.21717
AMB5.35	C. sp. nov. 1	Montagne d'Ambre	-12.49519	49.20783
ANJZ1	C. crossleyi	Anjozorobe	-18.4775	47.93812
ANJZ2	C. crossleyi	Anjozorobe	-18.4775	47.93812
ANJZ3	C. crossleyi	Anjozorobe	-18.4775	47.93812
JOZO4.7	C. crossleyi	Anjozorobe	-18.46789	47.94131
JOZO4.8	C. crossleyi	Anjozorobe	-18.46789	47.94131
JOZO4.9	C. crossleyi	Anjozorobe	-18.46789	47.94131
JOZO4.10	C. crossleyi	Anjozorobe	-18.46789	47.94131
MIZA16	C. crossleyi	Maromizaha	-18.97375	48.46461
MIZA19	C. crossleyi	Maromizaha	-18.97067	48.46431
MIZA6.1	C. crossleyi	Maromizaha	-18.95694	48.49236
MIZA6.2	C. crossleyi	Maromizaha	-18.95694	48.49236
MIZA7.1	C. crossleyi	Maromizaha	-18.95694	48.49236
TAD4.10	C. crossleyi	Mantadia	-18.80942	48.42731
TAD4.11	C. crossleyi	Mantadia	-18.80942	48.42731
TAD4.12	C. crossleyi	Mantadia	-18.80942	48.42731
TOR6.2	C. crossleyi	Torotorofotsy	-18.83658	48.34719
TORO8.11	C. crossleyi	Torotorofotsy	-18.77044	48.42814
TORO8.16	C. crossleyi	Torotorofotsy	-18.76856	48.42475
TVY7.12	C. crossleyi	Ambatovy	-18.85086	48.29256
TVY7.196B	C. crossleyi	Ambatovy	-18.86433	48.31136
TVY7.197	C. crossleyi	Ambatovy	-18.86658	48.30972
TVY7.199	C. crossleyi	Ambatovy	-18.87294	48.305
TVY7.20	C. crossleyi	Ambatovy	-18.84797	48.29433
ΓVΥ7.200	C. crossleyi	Ambatovy	-18.86883	48.30975
ΓVΥ7.206	C. crossleyi	Ambatovy	-18.87289	48.30453
ΓVY7.207	C. crossleyi	Ambatovy	-18.87178	48.30297
ΓVΥ7.22	C. crossleyi	Ambatovy	-18.85017	48.292
ΓVΥ7.33	C. crossleyi	Ambatovy	-18.85086	48.29256
ZAH240	C. crossleyi	Zahamena	-17.48917	48.74722
TRA8.81	C. sp. nov. 2	Andringitra (Ambarongy)	-22.22269	47.01889
TRA8.82	C. sp. nov. 2	Andringitra (Ambarongy)	-22.22292	47.0195

Table continued on next page

Table 1, continued

ID	Species designation	Location	Latitude	Longitude
RANO229	C. sp. nov. 2	Ranomafana (Talatakely)	-21.24833	47.42406
RANO2.95	C. sp. nov. 2	Ranomafana (Vatoharanana)	-21.2925	47.43842
KAL7.7	C. lavasoensis	Kalambatritra (Sahalava)	-23.53672	46.5335
POLO5.2	C. major	Tampolo	-17.28989	49.40753
ZOM6.2	C. medius	Zombitse	-22.88631	44.69375
GAR8	CCS2*	Manongarivo	-14.02369	48.27233
ANK5.18	CCS6*	Ankarana	-12.96631	49.13808
ANK5.19	CCS6*	Ankarana	-12.96631	49.13808
ANK5.20	CCS6*	Ankarana	-12.96631	49.13808
ANK5.21	CCS6*	Ankarana	-12.96631	49.13808
FIA5.19	CCS6*	Andrafiamena (Anjakely)	-12.91539	49.31956
FIA5.22	CCS6*	Andrafiamena (Anjakely)	-12.91539	49.31956
MATY5.31	CCS6*	Analamera (Ampasimaty)	-12.76556	49.48358
MATY5.40	CCS6*	Analamera (Ampasimaty)	-12.76703	49.48358
MATY5.42	CCS6*	Analamera (Ampasimaty)	-12.77136	49.48303
JOZO4.17	C. sibreei	Anjozorobe	-18.46789	47.94131
Thiele et al. 2013 Sam	ples (Fig. 5)			
AH-04-131	C. lavasoensis	Ambatotsirongorongo	-25.0780	46.7824
AHMG-06-201	C. lavasoensis	Grand Lavasoa	-25.0891	46.7447
AH-X-00-181	C. lavasoensis	Petit Lavasoa	-25.0809	46.7622

^{*} CCS designations 2 and 6 are from Lei et al. (2014).

engaged in pastoral activities (predominantly cattle grazing) (Cornell University/USAID/FOFIFA/INSTAT Census 2001). Timber extraction, quarrying, and land clearance for cattle grazing are also threats to the endemic wildlife. These threats have been exacerbated by rapid population growth, low levels of education, and extreme poverty; factors that have led the human population to devastate the ecosystem to obtain needed resources (Gezon and Freed 1999; Marcus and Kull 1999; D'Cruze *at al.* 2008).

Genetic samples, measurements and photographs of several sedated *Cheirogaleus* individuals were taken prior to their release (Table 2). The samples taken from these animals were subsequently analyzed in the context of a larger phylogenetic study of the genus *Cheirogaleus* by Lei *et al.* (2014), and determined to be sufficiently distinct to warrant elevation as a new species in the *C. crossleyi* species group. The Montagne d'Ambre individuals were designated *Cheirogaleus* sp. nov. 1 by Lei *et al.* (2014), as were six other "confirmed candidate species" (CCS) that likely warrant elevation to full species status. Here we describe a new species of dwarf lemur endemic to the area around Montagne d'Ambre.

Methods

Methods used to identify this new species were presented in Lei et al. (2014). Briefly, extracted genomic DNA taken from safely immobilized animals was subjected to a series of wet bench and computational analyses (Table 2). The mitochondrial regions analyzed were: Cytochrome b (cytb) (Irwin et al. 1991); Cytochrome oxidase subunit II (COII) (Adkins and Honeycutt 1994); the displacement loop or control region (D-loop) (Baker et al. 1993; Wyner et al. 1999); a fragment of the Cytochrome oxidase subunit III gene (COIII); NADH-dehydrogenase sub units 3, 4L, and 4 (ND3, ND4L, and ND4); and the tRNAGly, tRNAArg, tRNAHis, tRNASer, and partial tRNA^{Leu} genes (PAST) (Pastorini et al. 2000). Three nuclear loci were also sequenced: alpha fibrinogen intron 4 (FIBA), von Willebrand Factor intron 11 (vWF), and Cystic Fibrosis Transmembrane conductance (CFTR-PAIRB) (Heckman et al. 2007; Horvath et al. 2008). All genetic data were then analyzed using Maximum Likelihood (ML) and Bayesian phylogenetic analyses, and subjected to a battery of tests to examine the strength of the results (Lei et al. 2014). Phylogenetic trees were constructed based on these analyses and used to evaluate genetic divergence between lineages (Lei et al. 2014, Figs. 2-6, Appendix Ia-Id).

A Bayesian species delimitation analysis was performed using the bPTP webserver with 100,000 Markov Chain Monte Carlo generations, which is sufficient for datasets of less than 50 taxa (http://species.h-its.org; Zhang *et al.* 2013). The bPTP server uses a Bayesian Poisson tree processes model to add Bayesian support values to proposed species lineages on a

user-supplied tree using the number of mutations in a lineage. The mitochondrial combined guide tree included representative populations from the total sample set of Lei *et al.* (2014), with all individuals sampled at Montagne d'Ambre (*Cheirogaleus* sp. nov. 1) and all other individuals in the *Cheirogaleus crossleyi* group (*C. crossleyi*, CCS2, *C.* sp. nov. 2). Representatives from the other *Cheirogaleus* species groups (*C. lavasoensis*, *C. major*, *C. medius*, *C. sibreei*), as well as *Microcebus berthae* as an outgroup species, were also included in the bPTP analyses (Fig. 2).

Additionally, D-loop sequences were generated from fecal samples collected in February 2015 from Montagne d'Ambre (locations marked on Fig. 1), which were identical to those from blood and tissue samples. Because of the identical nature of these samples, they were not used in the analyses. The pelage of *Cheirogaleus* sp. nov. 1 was also compared to closely related species (Figs. 3 and 4).

Results

In the cytb sequence fragment analyses, Cheirogaleus sp. nov. 1, differs from its closest genetic relatives in Lei et al. (2014) (CCS2, CCS3, C. lavasoensis and C. crossleyi) in genetic distance by 5.6%±0.7%, 6.3%±0.7%, 8.1%±0.8% and 6.2%±0.6%, respectively. Despite being relatively geographically close to CCS6, with the Irodo River as a barrier, C. sp. nov. 1 is distinct from CCS6. The latter is clustered in the "Medius" subgroup clade with a genetic distance of 11.7%±0.9% between C. sp. nov. 1 and CCS6. Additional analyses using the mitochondrial loci listed in the Methods section above resulted in C. sp. nov. 1 segregating as an independent lineage with a high degree of confidence, but the results with nuclear loci were less robust among lineages even when large geographic distances (up to 900 km) were a factor. This may be the result of a number of factors, including incomplete lineage sorting, ancient introgression, or the small size of the nuclear sample analyzed (Lei et al. 2014, Fig. 5, Appendix Ib–Ic). The mitochondrial and nuclear phylogenetic trees generated in this study are available in Lei et al. (2014, Figs. 2-6, Appendix Ia-Id).

The population aggregate analysis (PAA) results were congruent with those presented in Lei *et al.* (2014). We obtained a Bayesian PTP support value of 1.00 indicating an excellent probability of the likelihood that this lineage is an independent species based on the given mitochondrial dataset (Fig. 2).

Discussion

Sufficient mitochondrial genetic divergence was observed, in conjunction with differences in pelage, to warrant elevation of this population as a new species. Additional evidence used in elevating this population to species status was its geographic isolation from other populations of *Cheirogaleus*. *Cheirogaleus* sp. nov. 1 is found northwest of the Irodo River, and is isolated from other *Cheirogaleus* species by this boundary (Fig. 5). A similar geographical situation exists with the

Montagne d'Ambre mouse lemur (*Microcebus arnholdi*) and the Tavaratra mouse lemur (*Microcebus tavaratra*), with the Irodo River acting as a barrier between the two lineages; pelage differences are visible between these two *Microcebus* species as well (Mittermeier *et al.* 2010). Geographic

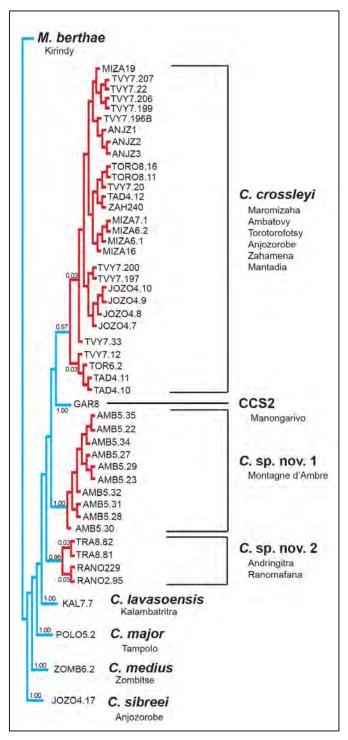


Figure 2. Results of the Bayesian species delimitation analyses of the combined mitochondrial dataset using the bPTP webserver (http://species.h-its. org). A total of 100,000 Markov Chain Monte Carlo generations were run with a rooted tree including the outgroup species *Microcebus berthae*. The Montagne d'Ambre population, site designation AMB (*Cheirogaleus* sp. nov. 1), had robust support (1.00) as an independent lineage within the *C. crossleyi* group.

Table 2. List of dwarf lemurs, *Cheirogaleus* sp. nov. 1, from Montagne d'Ambre examined during this study using site designation acronyms for specimens, AMB and DAMB, collected by Omaha's Henry Doorly Zoo and Aquarium (OHDZA) and Madagascar Biodiversity Partnership (MBP) field teams. Catalog and tissue accession numbers from the Museum of Texas Tech University (TTU-M).

ID No. Catalog No.	Catalog No.	og No. Tissue No.	Sex Microchip ID	Microchip ID	Weight (kg)	G	GPS	
AMB5.22			Male	466A1C1004	0.271	-12.52731	49.17331	11/21/2005
AMB5.23			Male	463D653640	0.256	-12.53017	49.17464	11/21/2005
AMB5.27	TTU-M 118801	TK 129239	Female	4669753C7D	0.310	-12.51722	49.17950	11/22/2005
AMB5.28			Female	466A1D6C48	0.391	-12.47881	49.21222	11/22/2005
AMB5.29	TTU-M 118802	TK 129240	Female	463B507D20	0.336	-12.47922	49.21606	11/22/2005
AMB5.30	TTU-M 118803	TK 129241	Male	467314576F	0.296	-12.47917	49.21597	11/22/2005
AMB5.31			Female	466C4A392F	0.311	-12.51083	49.19275	11/22/2005
AMB5.32*			Male	465E502450	0.110	-12.51242	49.18956	11/23/2005
AMB5.34			Male	462C017435	0.291	-12.47822	49.21717	11/22/2005
AMB5.35			Female	466C5E121D	0.321	-12.49519	49.20783	11/23/2005
DAMB15.4			Male	476F11225A	0.240	-12.52716	49.17191	02/28/2015
DAMB15.5			Female	47741F1E78	0.200	-12.52461	49.17236	02/28/2015
DAMB15.6			Male	4767432A7C	0.164	-12.52425	49.17302	02/28/2015

^{*}Juvenile

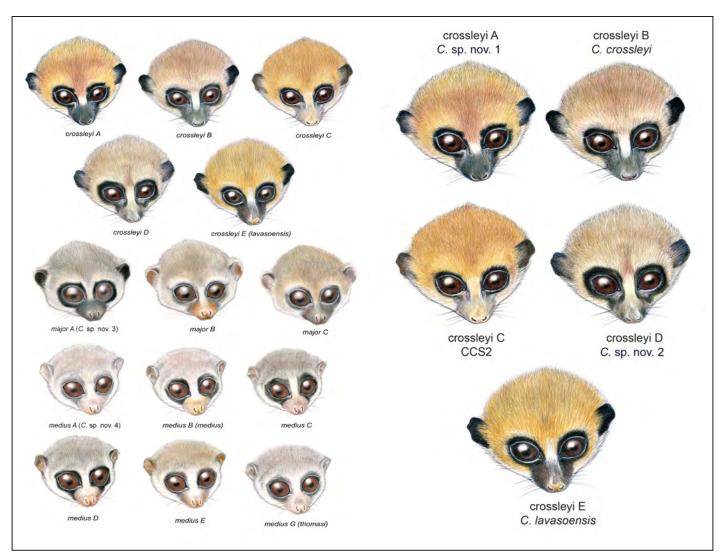


Figure 3. Illustrations of *Cheirogaleus* lineages based on archived photographs (Museum of Texas Tech University; Fig. 8 in Lei *et al.* 2014). Left panel represents all *Cheirogaleus* lineages, except *C. sibreei*. Right panel represents the *Cheirogaleus crossleyi* group, including *Cheirogaleus* sp. nov. 1, here named *Cheirogaleus andysabini*.

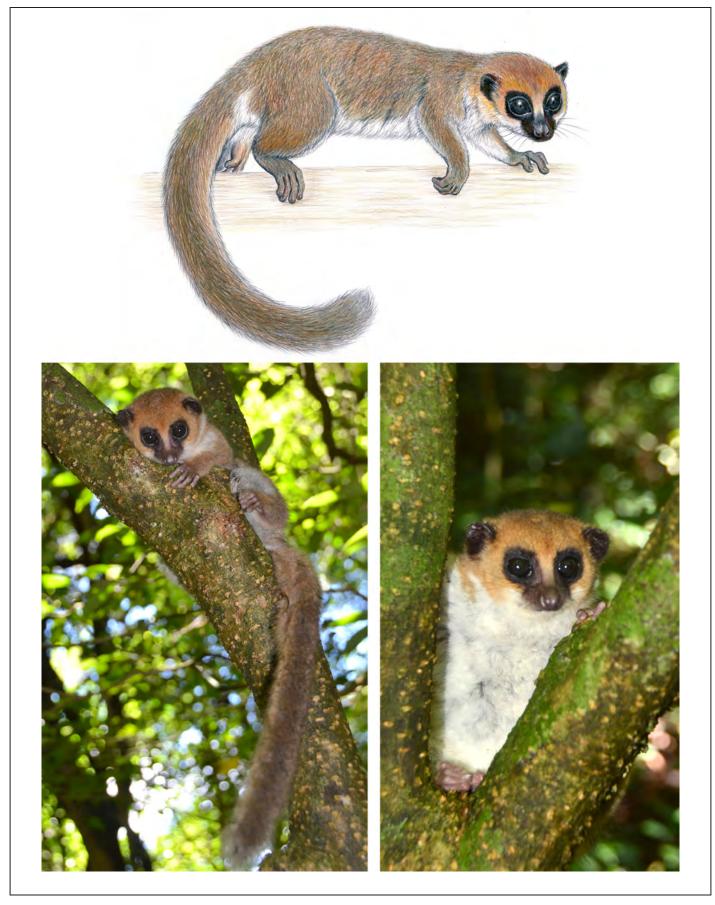


Figure 4. Illustration of *Cheirogaleus andysabini* and photographs of Omaha's Henry Doorly Zoo and Aquarium (OHDZA) catalogue acronym for specimen DAMB15.4 taken at Montagne d'Ambre. Illustrations by Stephen D. Nash ©Conservation International. Photographs by Edward E. Louis, Jr.

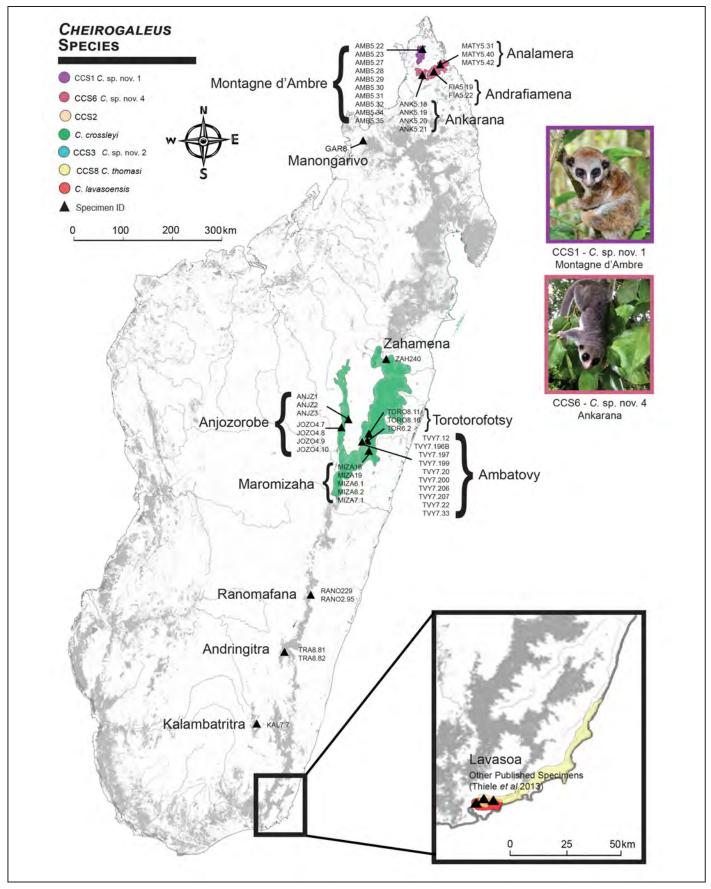


Figure 5. Map of Madagascar with the ranges of *Cheirogaleus* sp. nov. 1 (*Cheirogaleus andysabini*) and closely related *Cheirogaleus* species highlighted to show the geographic distance between lineages. ID numbers on the map correspond to ID numbers of animals listed in Table 1. Photographs of *Cheirogaleus* sp. nov. 1 and CCS6 (Lei *et al.* 2014), the Ankarana/Andrafiamena/Analamera/Bekaraoka lineage is provided to show a clear difference in pelage and the distance between the ranges of the two lineages. The Irodo River acts as a northern barrier to CCS6.

isolation alone is not evidence for the elevation of a new species. However, when considered as one factor alongside mitochondrial genetic divergence and pelage variation it provides additional justification for the description of a new species. *Cheirogaleus* sp. nov. 1 has a deeper reddish-brown dorsal coat, and a white rather than grey ventral coat that distinguish its pelage from that of the closely related *C. crossleyi* (Figs. 3, 4; See also Lei *et al.* 2014, Fig. 8). The average size of *C.* sp. nov. 1 is generally smaller than *C. crossleyi* individuals, although there is overlap in body size among some individuals (Lei *et al.* 2014, Table 4).

The Bayesian species delimitation analysis provided posterior delimitation probabilities in support of our elevation of the Montagne d'Ambre *Cheirogaleus* group as an independent species. We acknowledge the limitations of any species delimitation methodology when used independent of other corroborating methods (Carstens *et al.* 2013). In the case of this *Cheirogaleus* group the bPTP species delimitation is presented as additional evidence of our assertion that this group constitutes a new species.

Conservation Status

Insufficient information is available about the conservation status of this species, but the rate of anthropogenic ecological destruction in this region of Madagascar (and Madagascar overall) is severe. The population of this new species is found in and just outside the boundaries of Montagne d'Ambre National Park. A region of unprotected forest remains between the northern boundary of the national park and the Forêt d'Ambre Special Reserve (Mittermeier et al. 2010). The conservation status of this species cannot be determined at present, but the proximity to the park boundary and the settlement of Joffreville brings this species into close contact with humans and the possibility of forest clearance and hunting. The large port city of Antsiranana (formerly Diego Suarez) is c. 30 km away, and the demand for cooking charcoal from the sizeable population there has led to increased stress on the forest ecosystem at Montagne d'Ambre. Furthermore, the clearing of forest for the production of khat (Catha edulis) in the past decade has increased dramatically (E.E. Louis, Jr. pers. obs.). Therefore, with combinations of threats such as hunting, deforestation, and subsistence farming, even lemur populations in parks and reserves are not necessarily protected (Dufils 2003; Schwitzer et al. 2014). Given the microendemism found in Montagne d'Ambre, it is imperative to safeguard this habitat for this newly described Cheirogaleus species and other rare wildlife confined to this unique and isolated rainforest.

Cheirogaleus andysabini sp. nov.

Formerly *Cheirogaleus* sp. nov. 1, also CCS1 (Lei *et al.* 2014).

Holotype: AMB5.27 (AMB is the Henry Doorly Zoo designation for Montagne d'Ambre); adult female; Permit number 181; 4×2.0 mm biopsies from ear pinna and 0.3 cc

of whole blood; stored and curated at the Museum of Texas Tech University (MTTU, catalog number: TTU-M 118801/K 129239) Genetic Resources Collection, Natural Sciences Research Laboratory (NSRL); We placed a microchip subcutaneously between the scapulae and recorded as 4669753C7D; Collected by Jean Freddy Ranaivoarisoa, Ravaka Ramanamahefa, Nirina Jean de Dieu Andriamadison, Joseph Désiré Rabekinaja, Gérard Nalanirina, François Randrianasolo on 22 November 2005.

Paratypes: AMB5.28-5.32, 5.34-5.35, DAMB 15.4-15.6 Other specimens: Possible (unconfirmed), Harvard Museum of Comparative Zoology (MCZH) 44951, skull and skin from Montagne d'Ambre accessioned in January 1929 as part of the Grandidier Collection by Robert Barbour received from Louis Lavauden (missing in inventory since 1994). Additional specimen in the collection of the American Museum of Natural History (AMNH) M-100650, skull and skin taken in November of 1930 by Austin Rand at a site near Montagne d'Ambre "15 miles southwest of Tsarakimby."

Type locality: Madagascar: Antsiranana Province, Diana Region, District Antsiranana II, Montagne d'Ambre National Park, S12.52720, E49.17950 at 1073 m above sea level.

Measurements of holotype: Measurements (in cm and g) recorded in a field catalog: Body length 18.2 cm; Tail length 27.1 cm; Head crown 5.8 cm; Mass 310 g.

Description: The dorsum, limbs, and head are a rufous brown. The areas around the orbits are brownish-black, with a white patch proximal to the fleshy part of the nose in the inter-ocular space. The pelage on the ventral surface of the mandible is white, which is continuous onto the white pelage of the ventrum. Size is generally smaller than *C. crossleyi*, braincase higher, with very poorly expressed temporal lines (Fig. 4).

Diagnosis: *Cheirogaleus andysabini* can be distinguished from *C. crossleyi*, CCS2, CCS3 and *C. lavasoensis* by 10, 7, 10 and 16 apomorphic characters in the cytochrome b gene, respectively (Appendix II(k); Lei *et al.* 2014). *Cheirogaleus andysabini* has four diagnostic sites in the cytb sequence fragment such as G, A, G and G at the positions of 297, 303, 306 and 1071, respectively, which differentiate *C. andysabini* from all other *Cheirogaleus* species. Despite being geographically close to CCS6, with the Irodo River as a barrier, *C. andysabini* is distinct by nine diagnostic characters from CCS6, which is clustered in the "Medius" subgroup clade. An average weight of 0.282 ±0.61 kg, dark fur around eyes, rufous brown fur on dorsum, limbs, and head, venter is white. Table 3 contains measurements of captured individuals.

Distribution: *Cheirogaleus andysabini* is known from the Montagne d'Ambre National Park and areas nearby around the town of Joffreville, northwest of the Irodo River in northern Madagascar (Fig. 1). Observed at 541–1073 m above sea level.

Etymology: This new species is named after Andy Sabin, a well-known New York philanthropist committed to species conservation, especially turtles, amphibians and primates. In particular, he has supported many projects in Madagascar,

Table 3. Morphological data for adult Cheirogaleus species nov. 1, from Montagne d'Ambre

Class	No.	W (kg)	HC (cm)	HW (mm)	BL (cm)	TL (cm)	EL (mm)	EW (mm)	ML (mm)	MW (mm)	IW (mm)
Male	6	0.253±0.048	6.4±0.8	28.4±1.5	16.5±1.9	26.0±2.1	21.0±2.4	14.6±1.0	16.7±0.7	18.1±0.9	12.2±0.4
Female	6	0.312±0.062	6.0±0.5	27.6±3.2	17.1±1.5	26.4±2.3	22.2±1.6	15.0±2.4	15.0±0.2	18.5±1.0	12.0±0.8
Total	12	0.282±0.061	6.2±0.7	27.9±2.4	17.6±1.6	26.2±2.1	21.8±2.0	14.8±1.7	15.7±1.0	18.3±0.9	12.1±0.6

Note: W: weight; HC: head crown, HW: head width, BL: body length, TL: tail length, EL: ear length, EW: ear width, ML: muzzle length, MW: muzzle width, IW: intra-orbital width.

Table 3. Continued.

Class	F-Tb (cm)	F-LD (cm)	F-Hd (cm)	F-UR (cm)	F-H (cm)	H-Tb (cm)	H-LD (cm)	H-Ft (cm)	H-T (cm)	H-F (cm)	UC (mm)	LC (mm)
Male	1.1±0.0	1.4±0.3	3.4±0.2	4.1±0.4	3.5±0.7	1.6±0.2	1.5±0.2	5.0±0.1	5.2±0.5	5.7±0.5	3.2±0.3	3.1±0.4
Female	1.0±0.1	1.3±0.1	3.4±0.2	4.3±0.2	3.3±0.7	1.6±0.1	1.5±0.2	5.0±0.3	5.2±0.5	5.7±0.5	2.8±0.4	3.1±0.1
Total	1.0±0.1	1.4±0.2	3.4±0.2	4.2±0.3	3.4±0.7	1.6±0.2	1.5±0.2	5.0±0.2	5.2±0.5	5.7±0.5	3.0±0.4	3.1±0.3

Note: F-Tb: thumb (forelimb), F-LD: longest digit (Forelimb), F-Hd: hand, F-UR: ulna/radius, F-H: humerus, H-Tb: thumb (hindlimb), H-LD: longest digit (hindlimb), H-Ft: foot, H-T: tibia, H-F: femur, UC: upper canine, LC: lower canine.

including research on lemurs, tortoises and frogs. His longterm interest, his enthusiasm, and his generosity have helped to encourage many researchers and conservationists, young and old alike.

Vernacular names: Montagne d'Ambre or Andy Sabin's dwarf lemur.

Acknowledgments

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Home Range Size and Social Organization of the Sahamalaza Sportive Lemur, *Lepilemur sahamalazensis*

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Abstract: Knowledge of a species' social organization and spatial needs is essential to set up effective conservation measures. To date, there have been published studies on the home range size and social organization of only three of the 26 sportive lemur species currently recognized; there is no information available for the remaining 23. We studied home range size and social organization for the first time in the Critically Endangered Sahamalaza sportive lemur (*Lepilemur sahamalazensis*) by following eight radio-tagged individuals for 666 hours. Observations were made at night, recording interactions between them and the distances they travelled. Home ranges covered 0.38 ha and there was no overlap between adult individuals; nightly ranges were about 0.1 ha. Almost no social interactions were seen, and the very few observed sociopositive interactions took place between mother and kin, as suggested by size differences and diurnal observations. The small number of individuals observed makes conclusive inferences about the social organization of *L. sahamalazensis* difficult to make, but the low level of social interaction and cohesiveness shown indicates little social complexity and the possibility that they are essentially solitary.

Key Words: Critically Endangered, home range, Lepilemur, sociality, spatial needs, sportive lemur

Introduction

Following socioecological models, the distribution of animals in time and space is related to the distribution of restricted resources (Emlen and Oring 1977; Clutton-Brock 1989). Restricted resources for females (for example, food and safe sleeping sites) affect offspring survival, while the key resource for males is access to fertile females. The distribution of the different limiting resources, therefore, is believed to be associated with group size and movement patterns (Trivers 1972; Clutton-Brock and Parker 1992; Wrangham et al. 1993; Dunbar 1994). Females should only tolerate males (with whom they compete for food) if they profit from a permanent association with them (for example, by their defense of territories against rivals, by protection from infanticide, or by cooperation in parental care; see van Schaik and van Hooff 1983; van Schaik and Kappeler 1997). Site-related territoriality may evolve if feeding sites or safe sleeping sites are distributed in a manner that makes them defensible (Kaufmann

The size of a species' home range varies according to body mass, diet, sex, and age, and is also related to season, population density, group size, weather variables or habitat degradation and fragmentation (Burt 1943; Clutton-Brock and Harvey 1979; Harestad and Bunnell 1979; Haskell et al. 2002; Singh et al. 2001). Primate groups tend to be smaller and densities lower in secondary forests than in primary forests (Donati et al. 2011; Estrada and Coates-Estrada 1995; McCann et al. 2003; Schwitzer et al. 2007b). This suggests that a larger home range is necessary to sustain the same number of individuals in a secondary forest, and in the case of the lemurs this is most likely because larger home ranges are necessary for them to find sufficient food resources (Clutton-Brock and Harvey 1979; Robbins et al. 2006). Primate species that are ecologically flexible will be less affected by the loss of original habitat than those that rely on specific habitat characteristics or food resources present only in certain forest types (Andrianasolo et al. 2006; Ganzhorn and Schmid 1998; Schwitzer et al. 2007b).

The diversity of social systems of nocturnal prosimians is still not fully understood (Kappeler and van Schaik 2002). While some nocturnal species are pair-living, most appear to live in more complex societies where they rest in pairs or groups during the day but forage alone during the

night (Charles-Dominique 1977; Müller and Thalmann 2000). A number of species previously thought to be solitary are in fact pair-living (Fat-tailed dwarf lemur Cheirogaleus medius: Fietz 1999; Milne-Edwards' sportive lemur Lepilemur edwardsi: Thalmann 2001; Masoala fork-marked lemur Phaner furcifer: Petter et al. 1971; Schülke and Kappeler 2003; and Western woolly lemur, Avahi occidentalis: Thalmann 2003). It seems, however, that most nocturnal pair-living species differ in their degree of cohesiveness from diurnal pair-living primate species because males and females are only loosely associated (Müller and Thalmann 2000; Schülke and Kappeler 2003). In contrast to cohesive pairs that have frequent grooming bouts, small inter-individual distances and close coordination of the behavior of male and females (Müller and Anzenberger 2002), the "dispersed pairs" share the same home-range but are not continuously associated during their period of activity (for example, the Masoala forkmarked lemur: Schülke and Kappeler 2003). As dispersed pairs combine aspects of the likely evolutionary change of a solitary social organization to pair living, they may represent the earliest and most primitive form of sociality (Dröscher and Kappeler 2013).

The first field studies concluded that the typical mating system of solitary prosimians is most likely spatial polygyny; an adult male has access to the ranges of several females (Charles-Dominique 1977; Bearder 1987). More recent studies have identified other forms of polygyny (Kappeler 1997a; Eberle and Kappeler 2002). Müller and Thalmann (2000) concluded that the dispersed multimale-multifemale system and dispersed pair-living are the predominant patterns for solitarily foraging nocturnal primates and that dispersed harems (i.e., spatial polygyny) occur only seldom.

All sportive lemur species are now categorized as Vulnerable (4), Endangered (18) or Critically Endangered (4) on the IUCN Red List (Davies and Schwitzer 2013; IUCN 2014). The Sahamalaza sportive lemur is Critically Endangered (Davies and Schwitzer 2013; IUCN 2014), and was included on the list of the World's Top 25 Most Endangered Primates 2006–2008 (Olivieri et al. 2007a). The Sahafary sportive lemur, L. septentrionalis, occurring in far northern Madagascar, has been on the list of the World's 25 Most Endangered Primates since 2008. Despite this, home range size and social organization have been described for only three of the 26 currently recognized species. Zinner et al. (2003) found that male and female red-tailed sportive lemurs (Lepilemur ruficaudatus) occupied small home ranges (0.8 ha, 95% Kernel probability plots) that were stable over several years. While they form territorial pairs, the pair met only rarely except during the short mating seasons, and Hilgartner (2006) classified them as living in dispersed pairs. Milne-Edwards' sportive lemurs have similar home range sizes (Albignac 1981), but 3-4 individuals can often be seen feeding, without aggression, in the same tree, moving together for several hours, and grooming each other (Warren 1994). The mean home range size of females was recorded as 1.1 ha (Minimum Convex Polygons, MCP; Albignac 1981), with considerable home range overlap. According

to Thalmann (1998), Milne-Edwards' sportive lemurs live in dispersed family groups and are possibly pair-bonded. In a more recent study, it was described as pair-bonded, with the formation of stable sleeping associations between pair partners during the day and exclusive sleeping site and home range use (Rasoloharijaona *et al.* 2003, 2006). Reported mean home range size (MCP) was 0.98 ± 0.4 ha for females and 1.01 ± 0.25 ha for males (Rasoloharijaona *et al.* 2006).

In studies of the white-footed sportive lemur (*L. leu-copus*), most of the social units were found to be dispersed pairs, but some males were associated with two adult females (Charles-Dominique 1971; Dröscher and Kappeler 2013). According to Hladik and Charles-Dominique (1974) and Russell (1977), adult females defend a territory of about 0.18 ha, and adult males defend territories of about 0.30 ha. Grooming and the sharing of sleeping sites were not observed in these studies, and interaction tests even indicated active avoidance between pair partners (Dröscher and Kappeler 2013). There is no data for any other sportive lemur species.

Here, we report on our observations of home range size and social organization in the Sahamalaza sportive lemur, *Lepilemur sahamalazensis*. It is believed to be restricted to the Sahamalaza Peninsula in northwestern Madagascar (Olivieri *et al.* 2007b), an area that has experienced rapid and widespread deforestation. *Lepilemur* density in the Ankarafa forest, one of the three remaining forests in the species' distribution, ranged from 0.07 to 0.23 ind/ha (Seiler *et al.* 2013b). The smallest fragment where they occurred measured 10 ha.

In our earlier studies regarding their choice and use of habitats at night and in the daytime, we found that the lemurs actively chose sleeping sites and used home ranges according to habitat parameters that included high tree density, high level of canopy cover, and abundance of feeding trees and sleeping site trees (Seiler et al. 2013a, 2014). During the day, the lemurs rested alone in tree holes or dense tangles of vegetation up in the trees ("tree tangles") (Seiler et al. 2013a). Only mothers and babies (<2 months old) and mothers and infants (siblings from the previous year, <1 year) were observed to share sleeping sites. They were active for 5–14% of the daytime—autogrooming, being vigilant, and moving about—but never left their sleeping sites or fed. Owing to their exposed resting positions, these lemurs were easily accessible to diurnal predators, such as the Madagascar harrier hawk (Polyboroides radiatus), the fossa (Cryptoprocta ferox), and possibly the Madagascar tree boa (Sanzinia madagascariensis), as well as to human hunters (Seiler et al. 2013a).

An understanding of the species' social organization and spatial needs is crucial for an assessment of the habitat needs of this rare lemur, and furthermore might support conservation measures for all sportive lemurs. On the assumption that the home range would be similar in size to those of other sportive lemurs, we expected that *L. sahamalazensis* would use home ranges of approximately 1 ha. The likelihood was also that they are dispersed pair-living animals defending exclusive territories, and as such we expected to find home range overlap between certain adult male and female individuals and

minimal, if frequent, social interactions during their activity time. This would indicate similar-sized home ranges for males and females.

Methods

Study site

Ankarafa Forest is in the UNESCO Biosphere Reserve and national park on the Sahamalaza Peninsula, in the Sofia Region, northwest Madagascar (Fig. 1). It extends between 13°52'S and 14°27'S and 45°38'E and 47°46'E. The climate is strongly seasonal, with a cool, dry season from May to October and a hot, wet season from November to April. Ankarafa Forest lies in a transition zone between the Sambirano domain in the north and the western dry deciduous forest domain in the south. The forest is semi-humid with tree heights of up to 25 m (Schwitzer *et al.* 2006).

There are no large areas of intact primary forest left on the Sahamalaza Peninsula, and the remaining fragments all show some degree of anthropogenic disturbance and edge effects (Schwitzer *et al.* 2007a, 2007b). The forest fragments are separated by grassland with shrubs. Besides *L. sahamalazensis*,

the lemur community in Sahamalaza includes the blue-eyed black lemur *Eulemur flavifrons*, aye-aye *Daubentonia madagascariensis*, northern giant mouse lemur *Mirza zaza*, Sambirano lesser bamboo lemur *Hapalemur occidentalis*, and the fat-tailed dwarf lemur *Cheirogaleus medius*. All are threatened by hunting and forest destruction (Schwitzer *et al.* 2006). To date, the Sahamalaza sportive lemur has been confirmed only for this area.

Behavioral observations

Eight Sahamalaza sportive lemurs (seven females, one male) living in four forest fragments were fitted with radio-collars and followed during two field seasons (July–October 2009; April–August 2010). Mating activity has been described for the red-tailed sportive lemur (Hilgartner 2006) and Milne-Edwards' sportive lemur (Randrianambinina *et al.* 2007) as occurring in May and June, and we believed our field season would include the mating season of the Sahamalaza sportive lemur. We were unable to find further individuals that we were able to collar. The sportive lemurs were captured during the day at their sleeping sites (tree hole or tree tangle) with a blowpipe, using 1-ml, cold air-pressure, narcotic

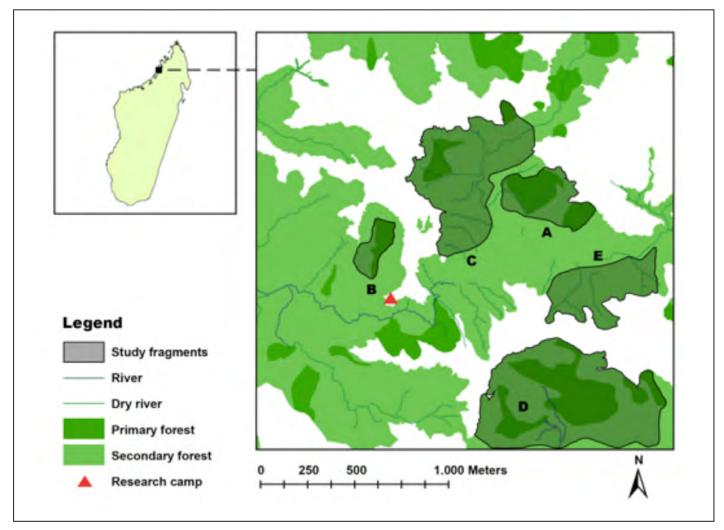


Figure 1. Study fragments (A–E) and the location of the research camp in the Ankarafa Forest, Sahamalaza Peninsula, northwest Madagascar. Fragments C and A are separated by a swamp, and low secondary growth (bushes, saplings) separate the other fragments.

syringe projectiles from Telinject (Römerberg, Germany). Lemurs were anesthetized for a short time to take body measurements (see Table 1) and equip them with radio collars. We used Ketasel 50 (50 mg Ketasel/ml) in the dose recommended by the manufacturer (0.01 ml/100 g body mass), but we had to increase the dose to 0.03 ml/100 g for three of the animals (large females). They were released after recovery at their capture site at the onset of their activity period. The animals captured were identified as adults by their body measurements and tooth profile.

In the first field season, TW3 brass-collar tags (Biotrack, Dorset, UK) were used. Smaller TW3 button cell collars (Biotrack, Dorset, UK), attached with cable ties for better adjustment, were used in the second field season. To make sure that the behavior of the collared individuals was not altered due to the collar, we observed five of them during the day (180 observation hours) and tested their levels of activity against the level of activity of un-collared individuals (N = 40, 1200 observation hours). There were no significant differences (Wilcoxon signed-ranks test: df = 45; Z = -0.943; P = 0.864). The radio collars were removed at the end of each field season, and most animals had gained weight compared to the first time we captured them (see Table 1), indicating that they were not agitated or disadvantaged by wearing them.

During night observations (18:00–06:00), the radio-collared lemurs were followed using a portable TR-4 receiver (Telonics; Mesa, Arizona, USA) during the first season, and a Biotrack receiver in the second season, a three-element yagi antenna (Biotrack, Dorset, UK) and a GPS device (GPS 60; Garmin Ltd., Schaffhausen, Switzerland). A new GPS location was logged every time the individual being followed moved to another location. If animals rested in one location

for a prolonged period of time, only one GPS data point was logged. We preferred this method to a periodical logging of location points as it was not always possible to locate an individual at all times. We conducted analyses of home range size and location via MapSource (version 6.13.7; Garmin Ltd., Schaffhausen, Switzerland). We estimated the overall home range per individual (N = 8) via 95% minimum convex polygons using all the location points of nocturnal follows per individual (Table 1). The method creates a polygon including all the locations where an individual was recorded (Mohr 1947), and it is possible that it calculates a larger home range when compared to Kernel density estimations. Most studies describing primate home range size use the MCP method, and we have used it to compare our results with those obtained for other species. To present a more detailed picture of the individuals' home ranges, we present the range sizes for each night in addition to the overall home range size.

Social behavior (recorded as instances of allogrooming, body contact, and agonistic behavior) and estimated distances to other sportive lemurs (if less than 15 m) were recorded continuously using focal animal sampling (Altmann 1974). "Near other" was also noted when the focal individual was out of sight but its location was known (for example, animal out of sight in the canopy of a large tree). We chose this method to avoid missing especially brief behaviors that are easily overlooked when using an interval observation method. In total, we followed the eight individuals at night for 666 hours (Table 1).

Data analysis

For comparisons of ranges covered during each observation night, we used a non-parametric Kruskal-Wallis ANOVA.

 $\textbf{Table 1.} \ \textbf{Body measurements (cm)} \ \textbf{and capture details of eight radio-collared adult} \ \textit{Lepilemur sahamalazensis}.$

	1	2	3	4	5	6	7	8
Individual	Male	Female	Female	Female	Female	Female	Female	Female
Body mass (g) at first capture	675	760	554	810	835	700	712	648
Head & body length	26	26	25	26.5	28	28,5	26	27
Tail	27.5	24	26	26.7	29	26	23	23.5
Nose-hindhead	5.5	5.47	5.27	5.2	6.09	5.42	5.9	5.87
Between ears	3.5	3.45	3.36	3.5	3.26	3.18	3.5	3.68
Femur	10.3	10.5	9	9.5	10.5	9	9	11
Tibia	10.6	10.5	10	10	10.5	10	10	10
Foot	7.7	6.8	7	6.8	8	7	7.2	7
Upper arm	6.2	6.5	5	7.5	6	6	7	6.5
Forearm	6.6	6.5	6.5	7.1	6	7	7	7
Hand	5	4	5	4.5	5.5	5.5	5	5.5
Weight of collar (g)	20	5	5	20	5	5	5	5
Study fragment	С	С	С	A	D	D	В	В
Capture date	3 Aug 09	15 May 10	17 May 10	3 Aug 09	18 May 10	19 May 10	14 May10	15 May10
Total night follows	11	5	6	11	6	6	4.5	6
Observation time (h)	132	60	72	132	72	72	54	72
Waypoints	987	438	701	1025	579	663	345	512
Out of sight (%)	74	46	32	69	46	28	33	47
Date of recapture	6 Jan 10	23 Sep 10	3 Jun 10	7 Jan 10	4 Jan 11	4 Jan11	5 Jan 11	3 Jun 10
Body mass (g) at recapture	702	782	538	874	834	715	762	639

When differences between individuals were statistically significant, we applied multiple Mann-Whitney-U tests with Holm's Sequential Bonferroni corrections as *post hoc* tests. The significance level α was chosen as 5% (P \leq 0.05). Statistical tests were carried out using SPSS 19.0 (SPSS Inc., Chicago, USA). As social interactions were very rare, we give an overview of the average number of interactions per hour but forego statistical comparisons.

Results

Ranging behavior

The lemurs had a median home range of 0.38 ha (Table 2; Fig. 2). The range covered in one night was 0.1 ha. There were no significant differences in range sizes covered in one night between the females, but the night range of the male was significantly larger than those of five of the females (Table 2). The largest home range was found for L5 (Table 2; Fig. 2); a female that rested in a tree hole or tree tangle on one side of a canyon during the day, which she would cross to spend the night on the other side of it, before returning to her sleeping site in the morning. But the variation in night ranges of female L5 were similar to those of the other females.

Social behavior

Home ranges of the collared individuals did not overlap (Fig. 3), but during night observations other, non-collared, individuals were occasionally spotted in the home ranges, indicating that individuals do overlap in their home ranges. Sometimes sportive lemurs were observed to be near (distance <15m) other sportive lemurs, but usually they did not interact (Table 3). In two cases, we saw sociopositive contact with another individual. On both occasions, the individuals approached each other and licked each other's faces. One of these meetings was between the collared male and a larger

female; the other between females of different sizes, which we think may have been a mother and daughter, as the collared female rested close to the other, smaller female during the day. Agonistic behavior towards other individuals—chasing other individuals without physical contact—was observed once for five, and twice for one of the eight lemurs (Table 3). Female L4 was observed to hit out towards another individuals' face with her hands when another individual approached the tree in which her baby was situated until the second individual fled. Body contact with allogrooming was observed only by mothers with their infants during diurnal observations, and is not considered here (see Seiler *et al.* 2013a). Five of the seven collared females had babies, born between mid-September and early October. We never observed any mating activity.

Discussion

Our preliminary results suggest that the observed Sahamalaza sportive lemurs have a low social complexity and might be solitary. They had exclusive territories of 0.38 ha with relatively small ranges of 0.1 ha per night and showed very little social interaction, probably largely between mother and kin.

Established home ranges might be important to minimize energy expenditures, which, being small folivores, might be of great importance to sportive lemurs (Kay 1984). During its resting period, *L. ruficaudatus* was found to have a markedly reduced metabolic rate (only 40% of the Kleiber value; Drack *et al.* 1999), probably to minimize energy expenditure (Ganzhorn 2002). It remains unclear if all sportive lemur species have a reduced metabolic rate during the day, especially when they are awake during their resting period, or if the metabolic rate is also reduced during their active period at night. Energy-saving strategies for the activity period should

Table 2. Home range size and median range per night (with quartile 1 and quartile 3) of eight *Lepilemur sahamalazensis* (L). Medians with different superscripts within a column differ significantly (Mann-Whitney U-tests with Holms-Bonferroni-Correction after Kruskal-Wallis ANOVA with α =0.05). Medians for all sportive lemurs are given in the last row.

Individual	L1	L2	L3	L4	L5	L6	L7	L8	ANOVA	Median
Home range (ha)	0.72	0.25	0.42	0.35	4.04	0.54	0.18	0.23		0.38 (0.27-0.59)
Nightly range (ha)	0.27 ^a (0.17-0.37)	0.12 ^{ab} (0.12-0.15)	0.07 ^b (0.03-0.09)	0.1 ^b (0.07-0.13)	0.05 ^b (0.02-0.11)	0.19 ^{ab} (0.1-0.22)	0.04 ^b (0.04-0.05)	0.09 ^b (0.06-0.09)	P=0.003, df=7 χ ² =21.868	0.1 (0.06-0.18)

Table 3. Total observation hours, hours in sight and amounts of social contacts of eight *Lepilemur sahamalazensis* (n/h with total numbers, for *Near other* based on total observation time, for further social behavior based on time in sight).

	Observation time (h)	In sight (h)	Near other (<15m)/h (total time)	Body contact/h (when in sight)	Agonistic/h (when in sight)	Allogrooming/h (when in sight)
L1 (male)	132	34.32	0.06(8)	0.03(1)	0.03(1)	0.03(1)
L2 (female)	60	32.4	0.09 (7)	0	0.03(1)	0
L3 (female)	72	48.96	0.019 (9)	0	0.02(1)	0
L4 (female)	132	40.92	0.19 (14)	0	0.02(1)	0
L5 (female)	72	38.88	0.08 (6)	0	0	0
L6 (female)	72	51.84	0.18 (13)	0.02(1)	0.03 (2)	0.02(1)
L7 (female)	54	36.18	0.22 (16)	0	0.03(1)	0
L8 (female)	72	38.16	0.1 (4)	0	0	0

nonetheless also be important for sportive lemurs and were found in a former study of *L. sahamalazensis* by Seiler *et al.* (2014). Energy saving might also explain the relatively small home ranges of sportive lemurs—about 1 ha for *L. edwardsi* (see Albignac 1981; Warren and Crompton 1997) and *L. ruficaudatus* (Zinner *et al.* 2003), and 0.18 ha for female and 0.33 ha for male *L. leucopus* (see Dröscher and Kappeler 2013). The much smaller grey mouse lemur (*Microcebus murinus*), with its broad diet, has similar home ranges of 0.7–1.6 ha for females and 2.8–4.8 ha for males in dry deciduous

forest (Eberle and Kappeler 2004; Lahann 2008; Radespiel 2000). With a median size of 0.38 ha, the home ranges of the Sahamalaza sportive lemurs we observed were similar in size to those found for the white-footed sportive lemur (Dröscher and Kappeler 2013). The animals only covered an average area of 0.1 ha in their home ranges during any one night. In our study, the only male animal in our sample covered a significantly larger range per night (0.27 ha) than did the females (0.09 ha).

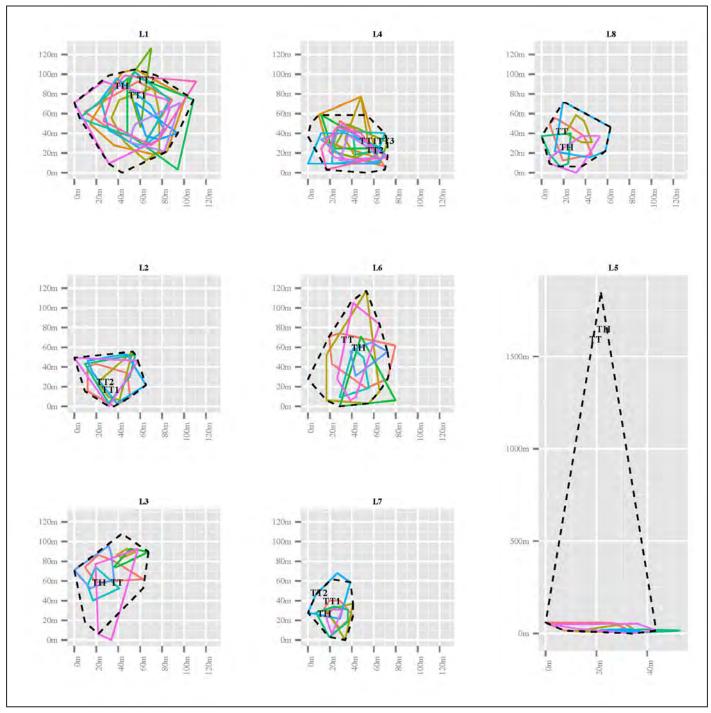


Figure 2a. Home ranges of seven females (L2–L8) and one male Sahamalaza sportive lemur (L1) during nocturnal observations. TH = tree hole, TT = tree tangle. Different colors mark the individual's home ranges on different nights. The overall home ranges are marked by dashed lines.

Because our observations were limited to just one male, we are unable to draw any firm conclusions concerning the social organization of L. sahamalazensis. The differences in night ranges between the male and the females could point towards a polygynous mating system, where adult males defend territories that cover those of 1–5 females, as has been described for L. leucopus by Hladik and Charles-Dominique (1974). Most of the social units of L. leucopus were found to occur in dispersed pairs, while some males were also associated with two adult females (Charles-Dominique 1971; Russell 1977; Dröscher and Kappeler 2013). Dröscher and Kappeler (2013) found very little social contact and active pair avoidance between pair-partners, and also that home ranges of males were substantially larger than those of females (0.33 ha vs. 0.18 ha), suggesting polygyny. Dröscher and Kappeler (2013) concluded that "the low cohesiveness together with extremely low rates of social interactions places the whitefooted sportive lemur at the low end of primate social complexity," a statement that is also true for our study on the Sahamalaza sportive lemur.

In general, we were able to observe individual sportive lemurs resting and feeding with relatively small distances between them, but social interactions were extremely rare and mainly agonistic (for example, chasing). The two allogrooming events we observed, most likely involved mother and offspring; one individual was slightly smaller than the other and we observed smaller individuals resting in proximity to the collared females that were known to have had offspring the previous year. In total, we observed 88 social interactions, including sitting separated by less than 15 meters. This was during 666 hours of night observations, resulting in only 0.15 social interactions per hour across all individuals. As we were not able to observe focal animals at all times during our night follows, this value should be considered as a minimum value and might be higher. However, this rate of observed social interactions is very similar to the 0.14 interactions/h across pairs recorded for L. leucopus by Dröscher and Kappeler (2013).

As individuals with little social contact may regulate their relationship with the help of vocal or olfactory signals, and

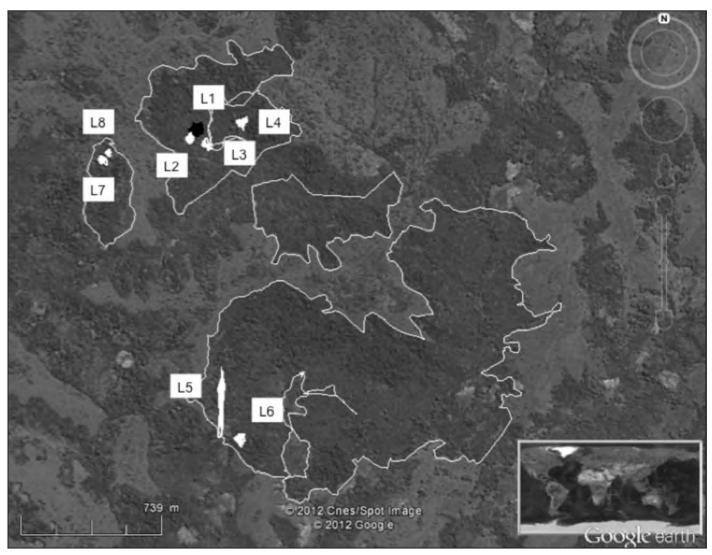


Figure 3. The home ranges of seven collared female (white) and one collared male (black) Sahamalaza sportive lemurs in relation to each other and the five forest fragments.

home ranges of certain male and female individuals overlapped in their study, Dröscher and Kappeler (2013) concluded that the white-footed sportive lemur lives in dispersed pairs. Sportive lemurs have been described as highly vocal (Rabesandratana 2006; Rasoloharijaona et al. 2006), and the use of loud calls for coordinating pair movements has been described for the pair-living L. edwardsi by Rasoloharijaona et al. (2006) and Méndez-Cárdenas and Zimmermann (2009). Lepilemur ruficaudatus on the other hand exhibited only a low rate of mutual (but not coordinated) vocal exchanges between pair-partners, suggesting that loud calling serves as a territorial signal and to regulate spacing (Fichtel and Hilgartner 2012), similar to what we found for L. sahamalazensis in another part of our study (Seiler et al. 2015). Lepilemur sahamalazensis vocalized only rarely (0.2 calls/h), and had a similar number (6, potentially 7, Seiler et al. 2015) of distinct call types to other sportive lemurs: L. edwardsi (9 call types) Rasoloharijaona et al. (2006); L. ruficaudatus (6 call types) Fichtel and Hilgartner (2012); and *L. leucopus* (5 call types) Dröscher and Kappeler (2013). The most frequent calls are likely to be either territorial or related to mother-infant communication (Seiler et al. 2015). We did not observe glandular scent-marking (or any forms of scent marking) or branchbashing displays such as those described for male L. leucopus by Dröscher and Kappeler (2013). We did observe individuals tree gouging when in their sleeping trees, resting. Tree gouging in weasel sportive lemurs (Lepilemur mustelinus) is thought to be used to register sleeping tree ownership (Rasoloharijaona et al. 2010). As this behavior often occurred after or during autogrooming in L. sahamalazensis, it is also possible that it is used to clean their mouth from hair.

Based on the very rare social interactions during the night, the solitary use of sleeping sites during the day, the low rate of loud calls, solitary use of home ranges and the lack of marking behavior, we believe that it is unlikely that the Sahamalaza sportive lemur is organized in dispersed pairs such as has been described for L. ruficaudatus and L. leucopus by Hilgartner (2006) and Zinner et al. (2003), respectively, or dispersed family groups with bonded pairs as in L. edwardsi (see Thalmann 1998). Our results rather point towards a solitary social system for the Sahamalaza sportive lemur, with home range overlap most likely only between relatives. In a solitary species "the general activity, and particularly, the movements of different individuals about their habitat are not synchronized" (Charles-Dominique 1978), resulting in solitary foraging of individuals (Bearder 1987) in contrast to gregarious animals, which synchronize their activity in space and time (Boinski and Garber 2000). Nonetheless, our data are not sufficient to draw definitive conclusions, and it is possible that more social interactions between adults during the night can be observed between November and early April, when we did not conduct observations.

As mating takes place in May and June in *L. ruficaudatus* and *L. edwardsi* (Hilgartner 2006; Randrianambinina *et al.* 2007, respectively), we assumed that the Sahamalaza sportive lemurs would also mate at this time. We never observed any

mating. In the first field season, we were able to observe that babies are born in September, which is about a month earlier than described for the other sportive lemur species. Considering a gestation period of 4–5 months for sportive lemurs (see, for example, Hilgartner 2006), we thus considered that the mating season for the Sahamalaza sportive lemur should be in April–May and started the second field season in April, but were not able to observe mating or increased social activity during that time, either. This might mean that mating took place but we failed to observe it, or that the mating season for the Sahamalaza sportive lemur is even earlier in the year, which would mean that the gestation period would have to be longer than 4–5 months. Studies over an entire year are needed.

Generally, the close overlap of male and female ranges including territorial defense against neighbors in many nocturnal primates, such as *L. edwardsi* (Rasoloharijaona *et al.* 2000; Thalmann 2001), *L. ruficaudatus* (Hilgartner 2006; Zinner *et al.* 2003), the Zanzibar galago *Galagoides zanzibaricus* (see Harcourt and Nash 1986), *Cheirogaleus medius* (Fietz, 1999; Müller 1998), and the fork-marked lemur *Phaner* (Charles-Dominique and Petter, 1980; Schülke, 2003), that lack constant associations between the pair partners, are thought to be examples of independent transitions from a solitary to a pair-living social organization (Kappeler 1999c; Kappeler and van Schaik 2002). The Sahamalaza sportive lemur might represent a very primordial example of social organization in primates.

The advantage of a solitary life style for the Sahamalaza sportive lemur, especially of resting alone during the day, could be explained by the high predation pressure in their nonactivity time and their sophisticated anti-predator behavior. The Sahamalaza sportive lemur shows considerable vigilance during the day, and listens to calls of surrounding species as well as predator vocalizations to react rapidly depending on the threat. By resting alone and freezing or fleeing into a tree hole, it minimizes the chances to be spotted by a predator (Seiler et al. 2013a). As a rather generalized herbivore feeding on at least 42 different and abundant tree species (Seiler et al. 2014), individuals should also not need a pair partner to help defend their food resources (resource defense theory; Brockelman and Srikosamatara 1984). Furthermore the paternal care hypothesis that assumes that the reproductive success of the female would suffer without help of a pair partner (Kleiman 1977; Clutton-Brock 1989) can be discarded for the Sahamalaza sportive lemur, as no male was ever spotted around mothers with youngsters or the youngster when left in a tree during the night (M. Seiler, pers. obs.). For the same reason, we can discard the infanticide-avoidance hypothesis, which assumes that infanticide is the primary force selecting for males associating permanently with one female unable to defend their infants against strange males (see, for example, van Schaik and Kappeler 1997). Seiler et al. (2015) reported that the observed female L. sahamalazensis with babies rapidly moved towards the tree that their babies were in when presented with the call type "2-parts", a possible mating call

of the species. We argued that it is possible that females will aim to avoid unknown males during the offspring care period. A case of infanticide at the onset of the offspring care period has been described for *L. edwardsi* by Rasoloharijaona *et al.* (2000). These observations suggest that females might indeed profit from a pair partner for infant protection, but our preliminary observations do not support that this is the case in the Sahamalaza sportive lemur.

Our results suggest that the Sahamalaza sportive lemur copes with this low energy diet by having relatively small home ranges. Though we cannot finally confirm this assumption, *L. sahamalazensis* might be the first-described solitary species in the genus *Lepilemur*.

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Ring-tailed Lemurs (*Lemur catta*), Forest Fragments, and Community-level Conservation in South-central Madagascar

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Abstract: The south-central highland region of Madagascar is largely deforested, except for rare, small forest fragments scattered across the landscape. Some of these fragments are now being managed by local community conservation associations, after village residents have seen, first hand, how decades of deforestation and, more recently, climate change in the region have affected their agricultural crops. Furthermore, ecotourism is becoming more common in this area, with the two largest fragments, Anja Community Reserve and the Tsaranoro Valley forest, frequently receiving both Malagasy and foreign visitors. The combination of revenue from such tourism and the prospects of greater food security (by conserving and expanding existing fragments, leading to better soil conditions for nearby crops and rice fields) has resulted in increased fragment preservation over the past few years. We surveyed seven of these fragments in August and September, 2013, with two goals: (1) to evaluate the viability of ring-tailed lemur populations in each fragment in relation to food and water resource availability; and (2) to discuss, with village conservation association leaders, the goals of each association regarding fragment conservation and benefits to local residents. Anja Reserve, operating since 1999, is highly successful, and the association's ecotourism and community development projects have won them national and international recognition. In 2012, village associations Sakaviro Miray, FI.MI.VA Samisorany, and Antokinihoavy-Andranobe received NGO funding to help build a tourism presence in the region, and infrastructure for such activities had begun when we visited these sites in 2013. The Tsaranoro Valley, where three of the fragments are located, is an adventure tourism destination; however, much of the tourism revenue goes to the owners of the trekking camps, although a portion of the funds are donated to the local Association Tantely each year, and these camps also provide jobs for local villagers. Recent efforts are underway to expand these three fragments via reforestation, and to create a corridor between two of them in order to assist with the dispersal of *L. catta* males, and thus assist with potential population gene flow.

Key Words: Community conservation, forest fragments, Lemur catta, south-central Madagascar

Introduction

In Madagascar, deforestation is considered exceptionally serious in the dry regions of the south (Bodin *et al.* 2006; Harper *et al.* 2007). Hannah *et al.* (2008) predicted that southern Madagascar will experience a mean temperature increase of 2.6°C in the 21st century, and that this largely arid region will become even drier, which will have important and largely negative biological consequences for its flora and fauna. Dry forest is the most fragmented forest type in Madagascar (Bodin *et al.* 2006; Harper *et al.* 2007), and in the south-central plateau (between Fianarantsoa and Andringitra National Park), continuous tracts of mixed deciduous, rupicolous, and dry-adapted forest—characteristic vegetation in this

region—are no longer present (Google Earth 2015; Cameron and Gould 2013). A combination of slash-and-burn agriculture, tree-cutting for fuel, and conversion to agricultural land over several centuries has resulted in a landscape composed of grassland, occasional small and scattered forest fragments, agricultural crops, and villages (Cameron and Gould 2013). The ring-tailed lemur (*Lemur catta*) is the only primate present in such fragments (Cameron and Gould 2013; Gould and Gabriel 2015), and one goal of our project was to evaluate seven fragments containing populations of this species in the south-central region, in relation to (1) forest and matrix quality (available food and water resources for the lemurs) and (2) lemur population viability (Gould and Cowen in prep.). Additionally, we consulted with five community associations

that are currently working with regional, national, and international NGOs to improve both forest fragments and agricultural crop quality, with the aims of (1) providing sustainable, secure food sources for the human inhabitants of this region, and (2) developing and maintaining eco-tourism sites in forest fragments managed by the communities, which could result in much needed financial benefits to the people in the region. In this paper we describe the efforts made by these communities, and we identify variables that can lead to successful community forest conservation, benefitting both humans and wildlife.

Study sites

The sites are located in a 220-km² mountainous region of south-central Madagascar, between Sakaviro Community Reserve, the northernmost fragment (21°47'03.86"S, 46°52'02.11"E), Marody forest (southern limit at 22°05'34.25"S, 46°47'39.57"E), Tsaranoro forest at the western boundary (22°05'10.74"S, 46°46'24.59"E), and Andranobe Community Reserve to the east (21°57'47.04"S, 46°56'43.84"E; Figs. 1 and 2). The fragments fall into two sub-regions: four in the Ambalavao region and three located in the Tsaranoro Valley (Fig. 2). Fragment altitudes ranged from 982 to 1117 m above sea level. Forest fragments in this region are characterized by granite outcrops surrounded by a combination of semi-deciduous and southern, dry-adapted, rupicolous vegetation (Randrianandrasana 2011; Gould and Gabriel 2015). The areas between fragments are made up of grassland, villages, rice terraces, and garden crops and, in the case of Anja, a small lake used for pisciculture (Cameron and Gould 2013).

Small forest fragments are highly vulnerable to biodiversity loss (Fahrig 2003; Gibson *et al.* 2013), and mammalian biodiversity in the fragments in which we worked was low compared to larger, intact dry forests of the southern, southwestern, and south-central regions, for example, Beza Mahafaly Reserve (Sussman and Ratsirarson 2006; Sussman *et al.* 2012), Berenty Reserve (Jolly *et al.* 2006; Jolly 2012), and the western side of Andringitra National Park (Bloesch *et al.*



Figure 1. Map of Madagascar indicating region where the study was conducted.

2002). *Lemur catta*, an extreme ecological generalist (Gould 2006), is the only primate found in these fragments. Local guides at each site stated that no nocturnal primates are found in these small forests, and our nocturnal survey of the largest fragment, Tsaranoro, revealed no sign of nocturnal lemur taxa. Larger predators such as fossa are absent, but we were told that a small carnivore locally known as "halaza" (likely the small Indian civet *Viverricula indica*) was present in most fragments, as are tenrecs (Family Tenrecidae).

Community-level Conservation Associations

We consulted with the following community-level associations: Anja Miray, Sakaviro Miray, FI.MA.VA Samisorany, Antokinihoavy-Andranobe, and Tantely. The first four are located in the Ambalavao region, and Association Tantely governs the villages and forest fragments of the Tsaranoro Valley (Fig. 2). Table 1 lists association names and years established, size (in hectares) of the fragments managed by each association, and approximate size of the *L. catta* populations in each fragment. We contacted the president of each association, and they and local guides accompanied us to the forests and assisted with the forest assessments and *L. catta* censuses.

We asked each association president the following questions: (1) what are the goals of the village association in terms of forest fragment conservation? (2) how will the community benefit from protection of the fragment? (3) are there plans for future fragment enhancement, for example, fragment expansion via reforestation, planting of potential vegetation corridors between fragments in close proximity, planting of trees in the matrix immediately surrounding the fragment that serve as food trees for *L. catta*? and (4) has the association received funding by an NGO to assist with the conservation program?

Association Anja-Miray (AMI) and the Anja Community Reserve

Established in 2000, the Anja Miray Association has been extremely successful in meeting its goals regarding forest conservation, and using monetary benefits from tourism



Figure 2. Location of each forest fragment visited during the study.

Table 1. Village associations and dates that each association was founded, fragment sizes, and population size of *Lemur catta* in each fragment as determined by census counts in 2013.

Village association (Communité de Base) and forest fragment name in English	Year association was established	Size of forest fragments managed by the associations (ha)	Approximate population size of Lemur catta found in each fragment in 2013 (adults and juveniles)	
Ambalavao region				
Anja Miray (Anja Community Reserve)	2000	36	210	
Sakaviro Miray (Sakaviro Community Reserve)	2012	14.2	30	
Association FI.MI.VA Samisorany (Samisorany forest)	2008	20.3	21	
Association Antokinihoavy- Andranobe (Andranobe- Andohabatonomby forest)	2012	Lower fragment=17.4 Upper fragment=20.7	Lower fragment=30 Upper fragment=6	
Tsaranoro Valley region				
Association Tantely (Tsaranoro, Chameleon, and Marody forests)	2002	Tsaranoro=46 Chameleon=8 Marody=2.8	Tsaranoro=78 Chameleon=28 Marody=15	

to help the community. The location of the Anja Community Reserve, just 13 km SW of the town of Ambalavao and immediately adjacent to Route Nationale #7 (21°51'09.44"S, 46°50'44.28"E), offers easy access to tourists, and Anja receives approximately 12,000 visitors each year, bringing in US\$35,000-\$45,000 annually (Rahaovilahy 2012). The main attraction is the large population of habituated ring-tailed lemurs (about 210-225 animals in 15 groups), and tourists can also view ancestral Betsileo tombs in the forest. Guides from the association lead tours and provide information on the history and cultural significance of the burial tombs, medicinal plants used by the Betsileo, and the behavior and ecology of the lemurs. AMI is composed of individuals from two villages who protect this 34-ha forest fragment for both community use and eco-tourism, the profits of which assist with community development and small-scale agriculture and pisciculture endeavors. In September 2013, AMI employed 85 guides and several trail managers. The association's successful conservation and development model has brought them regional, national and global recognition. In 2011, AMI won the national Communautés de Bases (COBA) prize as the best community association in Madagascar. The prize money was used for projects such as the construction of a school and distributing blankets to all elderly individuals in the region. In 2012, AMI was a recipient of the prestigious UNDP Equator Initiative Prize, awarded to just 25 development and conservation-based international projects every two years. AMI was selected as a finalist from over 800 entries worldwide. Also, in 2013, AMI was one of nine finalists competing for the NGO Argisud's regional agriculture prize.

Sakaviro-Miray, FI.MI.VA (Samisorany), and Antokinihoavy Andranobe

The 14.2-ha Sakaviro (21°47'03.86"S, 46°52'02.11"E), 20.3-ha Samisorany (21°47'11.35"S, 46°49'49.99"E), and 17.4-ha Andranobe (21°57'17.39'S, 46°55'36.44"E) forests are managed by the Communautés des bases (village associations) Sakaviro-Miray, FI.MI.VA, and Antokinihoavy Andranobe. The main objective of these associations is the conservation of the remaining forest fragments, in relation to both presence of water for successful agricultural yields,

and to attract eco-tourists, who provide revenue for village projects. There is also a second fragment at Andranobe, at a higher altitude than the main forest, which contained few lemurs, was partially degraded, and was not included in the ecotourism plan. The association members are highly motivated to receive tourists after witnessing the success of Anja-Miray. In 2011 and 2012, all three associations received funding from NGOs Haona Soa, Global Environment Facility's Small Grants Program (GEF), and Ny Tanintsika. Haona Soa is based in Fianarantsoa, and finances small community projects related to the conservation of remaining forest and small-scale agriculture. The GEF program provides "financial and technical support to projects that conserve and restore the environment while enhancing people's well-being and livelihoods" (https://sgp.undp.org). Ny Tanintsika is a collaboration of international sponsors working with the Malagasy government with the objective of combating poverty through an integrative approach involving protection of nature coupled with sustainable development as well as health initia-(http://www.feedbackmadagascar.org/fr/aboutus). tives The funding received from these NGOs has assisted the three community associations in establishing tree nurseries, constructing small tourist reception buildings, and erecting signs indicating the location of each site on major roads (Fig. 3). Furthermore, trails within the fragments have been established, and placards outlining the trail systems as well as regulations for tourists entering the forests have been posted at the entrances to the reception buildings. Tourists arrive at the reception office to pay the entrance and guide fees, and to meet with their guide, who then leads them on a tour of the forest. Although the ring-tailed lemurs in these forests are not as habituated to human presence as those at Anja, we noted that the two groups at Sakaviro, which had been operating for one year as of September 2013, were semi-habituated and tolerated the presence of tourists from approximately a 10-m distance (Fig. 4). Ring-tailed lemurs at Samisorany and Andranobe could be habituated if the associations are able to attract visitors interested in seeing their forests. In addition to lemurs, ancestral tombs decorated with zebu horns and remnants of historic dwelling walls are present at all sites, as well as artifacts preserved in rock shelters since at least the 19th

century (for example, potsherds, children's toys, cooking pots, fire rings, a prototype of the popular Fanarona board game at Sakaviro and, at Samisorany, a weaving loom). At all three sites, guides are eager to share stories of Betsileo ancestors, show visitors the artifacts that make up part of their cultural history, and find lemur groups for the tourists to view.

In 2003, there was a fire in the Samisorany area that destroyed a large tract of the forest in the region. In 2005, the villagers decided to protect the remaining forest and formed the Association FI.MI.VA Samisorany. Two species of *Ficus* (*F. megapoda* and *F. pyrifolia*) have since been planted in and at the edges of the fragment where maize was formerly grown.



Figure 3. Road sign indicating the location of the Sakaviro Community Reserve. NGO funding, which allowed for sign construction and tourism development, is acknowledged at the bottom of the sign.



Figure 4. Lemur catta juvenile at the Sakaviro Community Reserve.

In just a few years the forest has regenerated considerably, and few traces of the former crops can be found (Fig. 5).

Association Tantely and the Tsaranoro Valley forest fragments

The Tsaranoro Valley (22°05'10.83"E, 46°46'19.63"E), adjacent to the western border of the Andringitra National Park, contains three forest fragments that are managed by the Association Tantely: Tsaranoro, Chameleon, and Marody. The valley has become known over the past decade as a center for rock climbing and para-gliding, and has recently been included in Madagascar travel guidebooks. Ecotourism in the largest fragment, the Tsaranoro forest (46 ha), is growing tourists wishing to see ring-tailed lemurs (six groups totaling approximately 78 individuals), ancestral Betsileo tombs, caves, and a natural springs pool are accompanied by guides working for the trekking camps, and sometimes local guides. Association Tantely is composed of 11 villages. Toll fees are collected along the road leading to the Tsaranoro Valley, and this money is used for funding the Association's projects, such as trail maintenance inside the Tsaranoro forest, construction of fire breaks around Tsaranoro and the nearby Chameleon and Marody fragments, and road maintenance. The smaller Chameleon and Marody fragments (8.4 ha and 2.8 ha) could be used for ecotourism/lemur watching, as both contain small populations of L. catta, and Marody is situated very close to an exit trail from Andringitra National Park. Ecotourists trekking through Andringitra pass Marody on their way to the ecotourist camps and, since L. catta are difficult to locate in the vast and mountainous Andringitra Park area (31,160 km²), visitors hiking from Andringitra to Tsaranoro could potentially visit Marody to see the group of lemurs living in this small forest. Local villagers working with the guides from the Association Dyal (a guide association based in Ambalavao) are eager to conserve and further develop these fragments for tourism purposes.

In 2013, four ecotourism camps were operating in the Tsaranoro valley, catering primarily to foreign climbers and hikers. The owners of the camps—three French expatriates and one Malagasy (the second author P.A.)—donate part of their profits to Association Tantely. Projects funded by the camps thus far include construction of a church, school,



Figure 5. View of the 19-ha Samisorany forest fragment. The forest has regenerated well following a major fire in 2005.

medical clinic and village wells. Local villagers are employed in the camps in a variety of jobs, although the actual trekking/ climbing guides working at the camps are not from the valley.

Potential for community conservation success in south-central Madagascar

The associations with whom we worked were motivated to build an ecotourism presence in the south-central plateau region, particularly after witnessing the immense success of Anja Reserve. Anja has the advantage of an established 15-year tourism profile, and is visible from Route Nationale #7, just south of the town of Ambalavao. The smaller forests of Sakaviro and Samisorany are located further from the main highway, but if the community groups are able to promote their small forests via, for example, leaflets posted in the Ambalavao hotels, and being included in field guides and on travel websites, they could be successful, although to a lesser degree than Anja. The Andranobe Andohabatonomby reserve is found along a secondary road leading to Andringitra National Park, and could attract tourists headed for the national park if they engaged in some form of advertising.

Guides at Anja speak a number of languages, which is very helpful in terms of leading tours made up of foreign visitors. At Sakaviro, Samisorany, and Antokinihoavy-Andranobe, the guides speak only Malagasy, and this could pose a problem in terms of both promoting the forests and guiding foreign visitors, thus instruction in basic French, English, and German phrases (the three primary languages spoken by tourists to Madagascar) would be an asset. The Tsaranoro forest already receives quite a number of adventure tourists during the dry season, and the nearby Chameleon and Marody forests could easily become part of the forest tour, which currently includes only the larger Tsaranoro fragment. The guides working at the trekking camps do speak French and some English, but villagers interested in becoming involved with the ecotourism presence in the Tsaranoro valley would benefit greatly from learning basic phrases in both languages, so that they too could interact with tourists and benefit from tourism dollars.



Figure 6. Lemur catta climb along large boulders at the Anja Reserve.

Another important incentive for these communities to conserve and expand the forest fragments relates to increasing desiccation of arable land, caused by continuous deforestation and grass fires. Community presidents talked about the effects of local deforestation and resulting climate change. For example, in one community, previous rice yields were approximately 30 sacks per year, but in 2012, only eight sacks were harvested. Furthermore, locust plagues are more frequent in this region in the past few years, and crops have sustained serious damage from these insects. The loss of agricultural revenue has made local communities aware that without any forests, the very notion of food security will disappear, and this realization has sparked recent interest in the conservation and expansion of these small fragments.

Unfortunately, not all communities in the south-central region are motivated to conserve remaining small tracts of forests. We visited two other fragments, Bedita, near the Tsaranoro Valley (6 ha), and Ikomby (2 ha), three kilometers from Sakaviro Community Reserve, both containing very small L. catta populations. Both forests were severely degraded. At Bedita, villagers cut trees inside the fragment for firewood, and we found numerous remnants of recent fires set within the forest itself. At Ikomby, local people cut trees and collect considerable amounts of firewood at least once per week. We were told that while some of the local villagers near the Ikomby fragment want to conserve the small remaining forested area, others wish to continue harvesting the wood. These fragments are completely surrounded by anthropogenicallyproduced grassland, and the President of Association FI.MI. VA Samisorany mentioned that just 15 years prior to our visit, tracts of continuous forest were still present in this area.

The future of community managed forest fragment conservation in south-central Madagascar

The first author of this paper (LG) received a small grant from Conservation International's Primate Action Fund in 2013, and a portion of the funds were donated to the community associations of Sakaviro, Samisorany, Antokinihoavy-Andranobe, and Tsaranoro (Association Tantely) in August and September 2013 to (1) establish tree nurseries, the saplings of which will be planted at fragment edges to expand the small forests and provide more food trees for the resident ring-tailed lemur populations; (2) construct trail signs within each fragment; (3) clean and maintain the trails, making access easier for visitors; and (4) construct fire-breaks around some of the fragments, as grassfires set outside of the forests to encourage new grass growth for cattle often burn out of control in this region. As of October, 2013, the following actions had taken place. At Sakaviro Community Reserve, Samisorany and Tsaranoro, association members had begun to establish new tree nurseries to be planted for fragment expansion. In September 2014, a colleague of first author LG visited the Sakaviro Community reserve, and sent a photo of a thriving tree nursery, partially funded by the money that we provided to the Sakaviro Miray Association. The saplings grown in this nursery will be planted at the perimeters of the

reserve (P. J. Perry pers. comm). In June, 2015, second author (PA) noted that while some trees had been planted between the Tsaranoro and Chameleon fragments, rice growers in the valley did not want trees infringing on the rice terraces situated between the two forests, so it is unclear whether planting a connecting corridor will be possible.

In the Tsaranoro Valley forest, removal of the parasitic Cissus quadrangularis vine, Veldt grape, which had encroached upon the eastern part of the forest, had commenced, and a tree nursery was in the planning stages—the resulting saplings will be planted between the eastern edge of Tsaranoro and the southwestern edge of the Chameleon fragment. The distance between these two fragments is just 0.8 km, and such expansion could facilitate L. catta male dispersal between fragments. This is especially important, because while Clarke et al.'s (2015) examination of L. catta population genetics at Anja, Tsaranoro and Sakaviro revealed moderate levels of genetic diversity, the authors caution that these populations may be exhibiting a time-lag response before significant loss of genetic diversity occurs in the near future, due to extreme population fragmentation and the inability, in most cases, for male L. catta to disperse. In the small Marody forest, a sign indicating the trails within the fragment had been posted.

The management and development of ecotourism activities in some of the remaining forest fragments in this region has engendered local pride regarding endemic flora and fauna, and fostered an awareness of the importance of forest conservation. The establishment of these community conservation projects has brought extra income, and in some cases, national and international recognition for these local associations. We hope that the initiatives and projects described in this paper will continue and thrive so that the local communities, the remaining forest fragments, and the ring-tailed lemur population living within the fragments in this region of Madagascar will benefit in years to come.

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Expanding Knowledge on Life History Traits and Infant Development in the Greater Bamboo Lemur (*Prolemur simus*): Contributions from Kianjavato, Madagascar

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Abstract: Data are lacking on intraspecific variability in life history traits for the Critically Endangered greater bamboo lemur (*Prolemur simus*). Until now, detailed investigations on wild individuals had only been published for Ranomafana National Park, limiting the predictive power on the greater bamboo lemurs' possible responses to threats such as habitat loss and climate change. In this study, data were compiled on vital statistics and basic aspects of infant development for a 48-month period in Kianjavato, Madagascar. The area is mixed-use lowland forest with dense pockets of bamboo amid a disturbed landscape. Four core social groups, which would frequently coalesce into two larger groups, were monitored intensively. The birth pulse occurred in mid-to late September, nearly one month earlier than in Ranomafana National Park. Interbirth intervals and rates of attainment of infant developmental landmarks such as locomotor independence and weaning are discussed. Infant mortality averaged 47% with most deaths concentrated in December and January, while adult mortality was low with most deaths occurring during the dry season. Annual female adult mortality ranged from 0% to 22%. The mortality of adult males could not be assessed due to their dispersal.

Key Words: infant development, infant mortality, interbirth interval, life history, vital rates

Introduction

Knowledge on basic life history traits is a stepping-stone to the effective conservation of endangered species as well as an exploration of evolutionary and ecological questions. For organisms with long generation times, developing a comprehensive understanding of their life history requires long-term commitment of resources and personnel. Studies can continue for decades, as in the monitoring efforts on ring-tailed lemurs (Jolly et al. 2002; Gould et al. 2003) or Verreaux's sifaka (Richard et al. 2002). In great apes, Gombe's chimpanzees have been tracked for more than 50 years (Pusey et al. 2007), and Rwanda's mountain gorillas (Stewart et al. 2005) and Borneo's orangutans (Galdikas 1988) have been studied for more than 40. The opportunity for research of this nature on Madagascar's greater bamboo lemur (Prolemur simus) was uncertain as there were no reported sightings of this species in the twentieth century until 1964 (Meier and Rumpler 1987). Pivotal field studies in the late 1970s and 1980s identified two populations of P. simus in southeastern Madagascar in Ranomafana and Kianjavato (Petter et al. 1977; Meier and

Rumpler 1987; Wright *et al.* 1987), enabling future investigations on life history values that will contribute to the protection of greater bamboo lemurs in their native habitat.

The greater bamboo lemur is once widely distributed across vast areas of Madagascar and is the most abundant lemur in the subfossil record (Godfrey and Vuillaume-Randriamanantena 1986; Godfrey et al. 2004). The extensive historical range of *P. simus* suggests that it was well-adapted to this island nation's natural disturbance regime marked by cyclones, re-occurring droughts, and generally unpredictable precipitation patterns (Wright 1999; Dewar and Richard 2007). However, the recent decades of deforestation coupled with hunting are believed to be the leading causes of the greater bamboo lemurs' near disappearance, resulting in its classification as Critically Endangered (Mittermeier et al. 2010; Andriaholinirina et al. 2014). Recent surveys have located previously unknown populations, but this species is today restricted to pockets in the eastern humid forests (Andriaholinirina et al. 2003; Dolch et al. 2004, 2008; King and Chamberlan 2010; Rajaonson et al. 2010; Ravaloharimanitra

et al. 2011; Rakotonirina *et al.* 2011, 2013; Olson *et al.* 2012; Randrianarimanana *et al.* 2014).

Prolemur simus is an elusive, group-living, cathemeral lemur (Santini-Palka 1994; Tan 1999, 2000). Evidence of its presence at sites is often limited to signs of their feeding and to interviews with local people (Dolch et al. 2004; Ravaloharimanitra et al. 2011) as they are rarely encountered during site surveys. More than 3,000 human hours were invested at Torotorofotsy in the northern part of the species' current range to locate the first documented individual at this site (Dolch et al. 2008). Not only is the greater bamboo lemur difficult to locate, habituation is a lengthy process taking up to four times longer than for other bamboo lemur species (Tan 1999). Due to these obstacles, there are few sites with habituated groups of P. simus, and most published vital statistics and behavioral data are from a social group in the Talatakely parcel of Ranomafana National Park (Tan 1999, 2000; Bergey and Patel 2008). Additional information recently became available on more northerly groups (Bonaventure et al. 2012; Lantovololona et al. 2012; Mihaminekena et al. 2012; Randrianarimanana et al. 2012; Andrianandrasana et al. 2013; Randriahaingo et al. 2014).

Studies on wild P. simus have shown shown that it is a seasonal breeder, with births mostly confined to October and November at Ranomafana (Tan 1999, 2000) and near the villages of Ranomainty and Sakalava more than 350 km north in the Ankeniheny-Zahamena Corridor (Randrianarimanana 2012). These locations are all in eastern humid rainforests and at similar elevations, ranging from 900 m to 1160 m (Tan 1999; Randrianarimanana et al. 2012). Recorded gestation lengths in captivity (150 ±3 days; Roullet 2012) and at Ranomafana (148-150 days; Tan 2000) are consistent, and so most conceptions would evidently occur in May or June in the wild. At Ranomafana, females give birth to a single infant annually, having their first infant in their third year (Tan 2000). In captivity, estrus can begin as early as 1.5 years old, with the youngest individual giving birth at two years (Roullet 2012). Females are philopatric and males disperse when they are approximately 3.5 years old (Tan 2000). In captivity, males are removed from their natal groups at maturity at 2.5 years old when tensions with their father become apparent (Roullet 2012).

Differences in age of maturation in captive versus wild populations are likely related to provisioning, which has been reported to accelerate development (Altmann *et al.* 1993; Borries *et al.* 2001; Altmann and Alberts 2005). In Beza Mahafaly, for example, ring-tailed lemurs (*Lemur catta*) reproduce at three years old, while in Berenty where there are introduced food resources and provisioning, they have been seen to give birth when only two years old (Gould *et al.* 2003). The effects of provisioning in *P. simus* may be reflected in the recommended captive weights for males ranging from 2.7–2.8 kg (Roullet 2012), while the average weight for both sexes in the wild is 2.4 to 2.6 kg (Tan 2000, 2007).

Differences in infant maturation have also been noted in captive versus wild populations. In Ranomafana, infants were

weaned at 7.5 months old (Tan 2000) versus 8.5 to ten months in captivity (Roullet 2012). Accelerated infant maturation has been linked to nutritional stress at one end of the spectrum, but also to good ecological conditions on the other end of the spectrum (Lee 1996). It is likely that the prolonged period of lactation in captivity is also due to provisioning, especially as lactating females were possibly pregnant. Interbirth intervals are approximately one year in both the wild and captivity, and the total time of gestation plus nursing exceeds one year (Tan 2000; Roullet 2012).

Another aspect of infant development is the time of attainment of locomotor independence. Highly arboreal primate infants tend to have slower rates of physical development than more terrestrial species as arboreality has been implicated in promoting greater amounts of physical contact between primate infants and mothers (Chalmers 1972; Sussman 1977; Karssemeijer et al. 1990). Tan (2000) reported that P. simus in Ranomafana engage in many activities while on the ground and infants attain complete locomotor independence by 16 weeks of age. This would occur in February and March based on the birth pulse in October and November. Although not explicitly stated by Tan, locomotor independence coincides with a spike in terrestriality. Prolemur simus in Ranomafana spends up to 24% of its time on the ground in February (Tan 2000), and it is predicted that similar patterns of physical development will be seen in other populations of greater bamboo lemurs with infants becoming increasingly independent during periods of increased terrestriality. However, it is not expected that they will mature in this regard as quickly as the most terrestrial lemur species, Lemur catta, which spends up to 35% of its time on the ground. Lemur catta infants are skillful at leaping and playing by week eight, and increase locomotor independence during group travel by week ten (Gould 1990).

Although limited, the existing published baseline life history data on *P. simus* are extraordinarily valuable. Data on intraspecific plasticity of wild greater bamboo lemur populations are sparse, yet interpopulation variability has been identified as an important safeguard against extinction for mammal species (González-Suárez and Revilla 2013). The Ranomafana *P. simus* study population has declined since 2003 (Wright *et al.* 2008, 2012) to a current low of just two individuals in the park as reported in popular sources (Conway-Smith 2013; Douglas 2014) and reiterated at the *Prolemur simus* Working Group 2015 meeting. This draws attention to the pressing need of expanding knowledge on this species in its natural habitat and gathering data to facilitate exploration of local population declines (Cowlishaw *et al.* 2009).

This study's objective was to characterize basic life history patterns of a population of greater bamboo lemurs; monitoring wild, yet habituated, social groups living in a disturbed low-elevation evergreen humid forest in Kianjavato, Madagascar (McGuire *et al.* 2009). The submontane rainforests of Ranomafana are only 70 km west of Kianjavato, but the elevation drops as one descends from the eastern escarpment of the central plateau towards Kianjavato, and this change is

accompanied by shifts in weather (Donque 1972) that may affect seasonality and thus the life history patterns of wildlife populations. Our multi-year data set will provide insight into variability from the population level down to the individual. When possible, these data are compared to those from Ranomafana to assess intraspecific variation in life history parameters between different forest types and disturbance regimes. The data from this study can direct attention to factors affecting population viability in a critically endangered species.

Methods

All research was authorized by Madagascar's Ministère de l'Environnement et des Forêts, and was documented in a series of permits issued over the duration of the work (066/10/MEF/SG/DGF/DCB.SAP/SLRSE, 100/11/MEF/SG/DGF/DCB.SAP/SCB, 078/12/MEF/SG/DGF/DCB.SAP/SCB, 039/13/MEF/SG/DGF/DCB.SAP/SCB). All interactions with the study subjects abided by Omaha's Henry Doorly Zoo and Aquarium's IACUC (97-001, 12-101).

Study site and subjects

The Kianjavato Commune in southeastern Madagascar is characterized by a patchwork of lowland evergreen humid forest and agricultural land. At least 12 social groups of greater bamboo lemurs have been identified across the commune (Petter *et al.* 1977; Meier and Rumpler 1987; Wright *et al.* 1987; McGuire *et al.* 2009; this study). These lemurs are spread over an 8-km distance. An additional, but lesser known group, was observed at Tsitola at Kianjavato's western boundary near the Antaretra Commune. Of these groups, four were part of a long-term monitoring program begun at the end of 2010.

The monitoring program was focused primarily on *P. simus* social groups at the FOFIFA Kianjavato Coffee Plantation (21°22'43.2"S, 47°52'2.9"E), which is located on the southern aspect of the Sangasanga Mountain in Kianjavato Village (Fig. 1; McGuire *et al.* 2009). The monitored groups were referred to as West 1, West 2, East 1, and East 2. West 1 and West 2 frequently coalesced into a larger group, and the same was true for East 1 and East 2. The FOFIFA station includes areas of active agriculture near the mountain's base, progressing through secondary forest to a more mature intact forest near the summit approximating the less disturbed

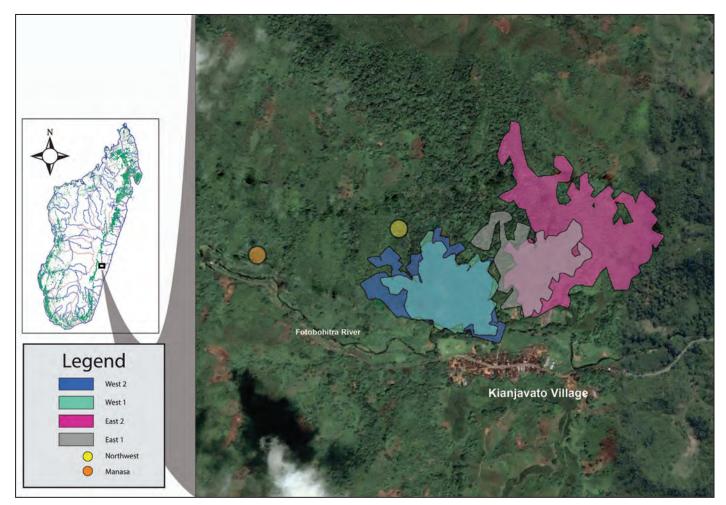


Figure 1. The study site was located on Sangasanga Mountain within the FOFIFA Kianjavato Coffee Plantation. The occurrence distributions of the four monitored *P. simus* groups are outlined, and the locations of two additional, nearby groups are indicated with circles. The northern side of Sangasanga Mountain was deforested.

vegetation found on the nearby mountain of Vatovavy. The forest at Sangasanga is used by residents of Kianjavato as a source of fuel wood, bamboo, and non-wood products.

Captures and measurements

Eighty-seven different immature and mature *P. simus* individuals were immobilized between 2000 and 2015 following methods described by Louis *et al.* (2006). Biomedical and morphometric data were recorded. Immature individuals less than three years old were identified based on size, weight, molar eruption and, when possible, known date of birth, and were excluded from calculations for average adult weight.

On first capture, microchips were placed subcutaneously into the interscapular space during the initial sedation to aid in the identification of each individual in ensuing recaptures. To facilitate monitoring, female greater bamboo lemurs in the behavioral groups were recognized by color combinations of nylon collars and aluminum pendants; male lemurs were outfitted with ATS radio collars (model M1545; Isanti, MN, USA).

Behavioral and census data

Behavioral data used in this study were collected by the authors from January 2011 through December 2014 from four habituated P. simus social groups. Censuses were recorded on behavioral groups a minimum of three to four times monthly during the behavioral monitoring program. Individuals received a score of zero if they were absent or one if they were present; presence of unknown individuals was always noted. These data were also used to calculate population growth rates (λ) as in Lawler (2011). Focal individuals were followed for two hours daily over three consecutive days every two weeks or monthly as the program expanded, such that data was distributed evenly for every individual throughout the monitoring duration. The hours of the follow per individual varied systematically to obtain behavioral data at different times during the diurnal portion of its activity cycle.

Data were recorded via instantaneous sampling at five-minute intervals (Altmann 1974), with rare behaviors recorded whenever they were seen (*ad libitum*). If an activity occurred on the ground during a scan, it was noted, and the percent of terrestrial observations per month was calculated. Activities recorded included resting, feeding (plant identification and part consumed), traveling, and social behaviors. Female-specific activities relating to interactions with infants were also recorded. The distance between mothers and infants was noted during the infant's first year of life, and three general categories were assessed: in physical contact, within one body length of mother, and greater than one body length away from mother but within visual and hearing distance. Occurrences of nursing or if the infant was mounted on the mother while she was moving were also recorded.

Life history data

Based on preliminary data from 2010, beginning the second week of September we checked *Prolemur simus*

females in the four core social groups every day for the presence of newborn infants. The daily checks, including weekends, continued for five weeks or until an infant was observed. If an infant was born after mid-October its presence was recorded during subsequent censuses, but resulting in less precise birth date estimates. Birthing seasons were identified by the year that the season begins with the caveat that the interval could continue into the following year. The midpoints between the first and last dates of possible parturition were used to calculate the interbirth interval (IBI) in days, which were converted to months as in Fürtbauer *et al.* (2010).

Prolemur simus females were often absent from their groups prior to the birth of an infant. All downstream calculations were, therefore, based on the average birth date of an individual, which was the day that fell between the last time a mother was observed without an infant and the first day she was seen with an infant. The week of birth was estimated to be the week including the infant's average birthdate with week 1 starting on January 1 (Tecot 2010). The week of conception was estimated by counting back 149 days from the average birth date—the average length of gestation reported in the wild (Tan 2000) and within the documented range for captivity (Roullet 2012).

Infants were presumed dead if mothers were repeatedly seen without them before the infants attained an age of one year. At Sangasanga, the adult female membership of a social group was consistent with no known incidences of immigration during the study period. Therefore, if an adult female went missing from a group she was considered deceased, although females and their offspring in Ranomafana have been noted to migrate on rare occasions (Wright *et al.* 2012). The male membership was much more fluid, with males frequently moving between groups, especially the subordinate males. Missing males were not considered deceased unless their remains were found.

Data analysis

Circular statistics are recommended for cyclical data (Berens 2009) and were used to determine seasonality in births. This method allows one to take into account the proximity of December 31st to January 1st, which would otherwise be on opposite ends of a linear scale. For this analysis, births were grouped according to month making the circular axis one year composed of 12 equal parts each 30°. Although the data were grouped, a correction factor was not calculated as this is not problematic for most applications as long as groupings are less than 45° (Jammalamadaka and SenGupta 2001). The R-package CircStats (Agostinelli 2009) was used and the Rayleigh test was implemented to check for seasonality. Yearly data from 2011 to 2014 were analyzed separately and then combined.

Results

Captures and measurements

In Sangasanga Mountain in Kianjavato, greater bamboo lemurs were immobilized in every month of the year except March between 2000 and 2015 (Table 1, Fig. 2). The average weight of an adult female *P. simus* at Sangasanga was 2.61 kg (range 2.20–3.25 kg; 48 measurements representing 29 individuals), and the average weight of an adult male was 2.75 kg (range 2.15–3.55 kg; 76 measurements representing 32 individuals). The average weight of males was significantly higher than that of females (t = 2.6353, df = 122, p <0.05), but the size difference was not readily observed in the field.

Behavioral data

In total, there were six groups of *Prolemur simus* with abutting territories occupying Sangasanga. Four of these groups were habituated and had in total from 29 to 55 individuals in 46 ha in 2014 (Fig. 1). The number varied throughout

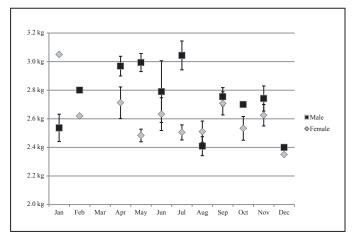


Figure 2. Averaged weights of captured male and female adult *P. simus* from the Kianjavato Commune by month from 2000 to 2015. See Table 1 for accompanying data.

the year due to births, deaths, and dispersals. Group composition is shown in Table 2. Overall, the population of the focal groups expanded 19.0% from 2011 to 2014. Lambda was 1.06 and 1.17 for 2012 and 2013, respectively, showing positive growth rates, but dropped to 0.99 in 2014 hovering near equilibrium. A combined total of 5788 hours of behavioral data were recorded.

Infants were in physical contact with their mothers for 100% of observations during the first two weeks of their life, declining to 83% on average by week five. Infants began spending more than 50% of their time out of physical contact with their mothers by week 12, typically occurring in mid- to late December (Fig. 3). Around this same time, infants were no longer dependent on their mothers to transport them, with the last observation of being mounted on their mothers during movement occurring on average at 11.8 weeks of age (n = 18, SD = 0.63); although simplistic, this was deemed to be the point of locomotor independence. Simultaneously, the percentages of observations occurring on the ground began to increase markedly in December, peaking in January with a high of 11.10% in 2013, and an overall average of 8.46% for this month. Average percent terrestriality decreased to less than 1% from June to September (Fig. 4).

Life history data

Females typically reproduced annually, giving birth to single infants. Two sets of twins were reported, however, in social groups outside of Sangasanga, but within the Kianjavato Commune. The average fecundity rate for the four social groups monitored from 2011 to 2014 was 94.0% ranging from 91.7% to 100.0%, and resulting in 45 births. These were minimum fecundity rates, as it was possible for an infant to be stillborn or to have died before its presence was noted. Two female greater bamboo lemur individuals became reproductively mature during this study and had their first infants during their third year, agreeing with previous reports (Tan

Table 1. Average weights of captured adult greater bamboo lemurs from Sangasanga, Kianjavato from 2000 to 2014.

	, e i							
Month	Female (kg)	Standard error	n	Male (kg)	Standard error	n		
Jan	3.05	0.00	1	2.54	0.10	6		
Feb	2.62	0.00	1	2.80	0.00	1		
Mar								
Apr	2.71	0.11	4	2.97	0.07	12		
May	2.48	0.04	3	2.99	0.06	7		
Jun	2.63	0.11	8	2.79	0.22	5		
Jul	2.51	0.05	6	3.04	0.10	12		
Aug	2.51	0.07	7	2.41	0.07	6		
Sep	2.71	0.08	12	2.75	0.06	13		
Oct	2.53	0.08	3	2.70	0.00	2		
Nov	2.63	0.08	2	2.74	0.09	11		
Dec	2.35	0.00	1	2.40	0.00	1		
Total			48			76		

2000). Also in his third year, one male dispersed from his natal group into an adjacent group as seen at Ranomafana (Tan 2000). Two additional males moved between closely linked subgroups in their third year, for example from West 1 to West 2, and then emigrated from their overall social group in their fourth year. It was not possible to calculate adult mortality for male greater bamboo lemurs as their disappearance from a group could be attributed to either death or dispersal. No females died in 2011 and 2014. One female died in 2012 (9.0%) and the remains were recovered. Three females died

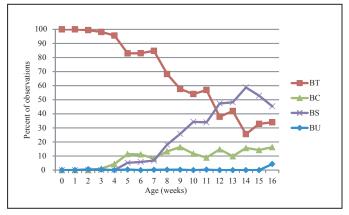


Figure 3. Proximity of an infant *P. simus* to its mother according to its age. BT – infant in physical contact with its mother; BC – infant within one body length of the mother; BS – infant greater than one body length from the mother but within sight or hearing distance; BU – infant's location is unknown.

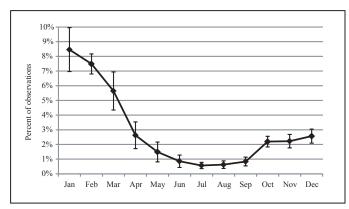


Figure 4. Percent of *P. simus* observations occurring on the ground by month with standard error of the mean.

in 2013 (22.0%), and the remains of two were found. The third was temporarily outfitted with a radio collar to assist with locating her during the birth season. The collar was cut and hidden in a small hole under a rock; she was considered a victim of poaching and her dependent infant was also lost.

Length of gestation, birth synchrony, and interbirth intervals

Birth dates were estimated, on average, to within a 7.8 day interval over four seasons and to within hours for exceptional cases. It was rare to have such narrow windows as *P. simus* females were often absent from their group for up to six days prior to returning with a new infant. The first of these exceptional cases was an infant born to a female 148 to 150 days after a witnessed copulation event. The narrowest birth window was 14 hours, 149 days after she mated with the dominant male of her group. This is in agreement with previously recorded gestation periods (Tan 2000; Roullet 2012).

Timing of births in Kianjavato showed significant seasonality (Rayleigh test: Z = 35.96, p < 0.05) with 20 of the 43 observed infants from 2011 to 2014 estimated to have been born in weeks 38 and 39, from mid- to late September (Fig. 5). Forty-five births were mentioned earlier in this text, but the birth dates of two infants could not be estimated due to a short disruption in the monitoring efforts due to unsafe field conditions. The average birthdate of infants to multiparous females was September 28 (n = 41, SD = 22.0) or 99 days after June 21st, which is the winter solstice in the southern hemisphere. The winter solstice was used as a reference point by Tan (2000), and so also used here to permit comparison. The average birth date occurs significantly earlier (two-sample t, df = 48, t-value = 4.06, p = 0.0002) in Kianjavato than in Ranomafana, where the average birthdate was 131 days after the winter solstice (n = 9, SD = 18.2; Tan 2000). Infants born to first-time mothers (n = 2) were not included in the calculation of average birthdates for Sangasanga as there is a general trend suggesting that estrus occurs later for P. simus primiparous females in comparison to multiparous females. For example, one female had her first infant in January, while another had her first infant near the end of November. By subtracting 149 days from the average birth date of infants born to multiparous females, most successful copulation events were found to occur during weeks 17 and 18, corresponding to the end of April and beginning of May (Fig. 5).

Table 2. Composition of *P. simus* study groups from 2011 through 2014. The number of animals in each age category was recorded monthly then averaged for each year.

	2011		2012		2013			2014						
	East	West 1	West 2	East	West 1	West 2	East 1	East 2	West 1	West 2	East 1	East 2	West 1	West 2
Adult males	6.3	3.0	2.0	5.9	2.3	2.0	3.5	3.3	2.8	2.0	4.3	2.5	2.0	2.3
Adult females	4.3	3.5	2.3	4.4	4.4	2.8	4.9	2.6	3.2	2.8	6.1	3.4	2.0	2.0
Juveniles & subadults	1.8	2.3	1.0	3.6	2.5	1.4	3.9	1.2	2.4	3.0	2.7	1.9	1.9	2.1
Infants	4.0	3.0	1.3	3.8	1.8	1.6	3.9	1.8	0.8	0.8	3.9	2.3	1.4	1.9
Total	16.3	11.8	6.5	17.7	11.0	7.8	16.3	8.9	9.1	8.6	16.9	10.1	7.3	8.3

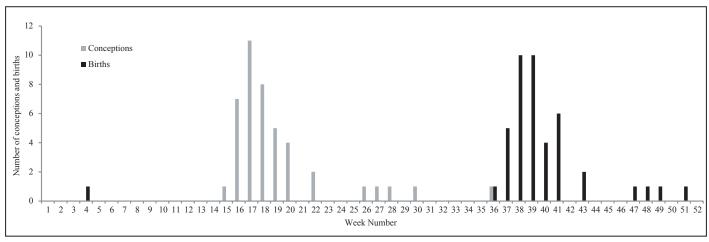


Figure 5. Distribution of conception and births for *P. simus* at Sangasanga, Kianjavato.

Average IBI of multiparous females from 2011 to 2014 was 363.7 days (n = 22, SD = 23.7). New mothers varied in the adjustment of their IBI to synchronize with the following year's birth pulse. One individual had a curtailed IBI of just 10.4 months between her first and second infant, while the IBI of another was reduced by a smaller increment to 11.0 months. The loss of an infant did not significantly influence the subsequent IBI (two-sample t, df = 20, t-value = 2.045, p <0.05), although a difference was observed with an average duration of 12.1 months if an infant survived (n = 11) and 11.5 months if an infant died (n = 13).

The IBI is influenced by lactation (Thompson *et al.* 2012); thus, it is useful to note that the age of weaning was roughly estimated to be the date nursing was last observed and on average occurred 7.0 months after birth (n = 14, SD = 0.98). During most of this time, infants were consuming milk as well as provisioning for themselves. The last date of observed suckling is a simplistic view of the weaning process (Lee 1996); however, it is unlikely the infants derived much of their nutrition from their mothers beyond this point even with occasional bouts of nursing.

Minimum infant mortality rates

Infant mortality in Kianjavato increased from 45.5% for the 2011 birthing season to 54.5% for the 2012 season. The mortality rate for infants born in 2013 was 40.0%, for an overall average infant mortality rate of 46.7%. As of December 2014, four of 13 infants died. Half of all infant deaths occurred in December and January, with an average age at death of 3.2 months (n = 24, SD = 1.64). An additional five infants died in March and April, perhaps related to weaning. No infants died between May and July.

Discussion

Conception and birth

Comparisons of data between and within populations of greater bamboo lemurs demonstrated previously undocumented plasticity in this species' life history. With conception and birth as the starting point for comparison, we found that the timing of birth pulses varied between greater bamboo lemur populations at Ranomafana and at Sangasanga, but was consistent within locales. The later average date of conception and, hence, birth pulse in Ranomafana may reflect adaptations to the different environments at these mid- and low elevation forests, respectively. The coolest months at both sites are from June to August with temperatures at Ranomafana dipping down to 4–6°C (Tan 1999) while dropping to only 11°C in Kianjavato (data from the local weather station).

The basal metabolic rate (BMR) is the minimum energy cost of living (Frappell and Butler 2004) and as ambient temperatures decrease, this cost of living increases for endotherms that must maintain a specific body temperature (Frappell and Butler 2004; Naya *et al.* 2013). The BMR also increases during pregnancy, and more so during lactation (Frappell and Butler 2004; Speakman 2008).

Additionally, cooler temperatures affect the assemblage of plant communities and timing of phenophases, affecting the availability of certain food sources. For example, *Cathariostachys madagascariensis*, an endemic woody bamboo, is the staple of the *P. simus* diet at Ranomafana (Tan 1999). This bamboo is associated with lower montane forests where it grows in disturbed areas or gaps (Dransfield 1998; King *et al.* 2013; Olson *et al.* 2013). In Kianjavato, *Valiha diffusa* is the dominant woody bamboo and the staple food of *P. simus* at Sangasanga (Tan 2007). This species grows in low elevation areas, frequently in highly disturbed habitats (Dransfield 1998; King *et al.* 2013).

In Sangasanga, the first infants of the birth season were observed during the second week of September, while births in Ranomafana were well synchronized and occurred one month later during October and November (Tan 1999, 2000). The delayed conception at Ranomafana, and therefore the birth pulse, may result in the increased BMRs of mothers coinciding with increasing food supplies and the onset of warmer weather. Shifting the birth pulse may also ensure that infants have a sufficient food supply when nutritionally independent,

as predicted with the classic reproductive strategy (Lewis and Kappeler 2005).

Infant developmental landmarks

The last observation of nursing in Sangasanga was recorded on average 7.0 months after birth, or 213 days, which is typically late April. In Ranomafana, infants were weaned at 7.5 months (Tan 2000), which should be around early June. A statistical comparison was not possible between these two sites due to limited information on the Ranomafana population. We do not predict, however, that these time frames were significantly different, as multiple infants at Sangasanga did nurse for a similar duration. In Sangasanga, weaning coincides with the consumption of the fruits of a native palm, Dypsis sp., as well as the fruits of the alien invasive herb Clidemia hirta (this study). Both of these food sources are accessible to infants, in contrast to woody bamboo culms or the large tips of new culms that require the strength of an adult to break. Although these fruits only constitute less than 10% of the adult diet from February to June (this study), they may be important for infant nutrition. More detailed observations on immature individuals would be necessary to address differences in diet between adults and infants as they develop.

The attainment of locomotor independence occurred over a protracted period in Sangasanga (n = 18) in comparison to Ranomafana (n = 9), which may, in part, be related to sample sizes (Fig. 6). On average, infants in Sangasanga traveled independently of their mothers (but with the group) at 2.8 months, or nearly 12 weeks of age, typically mid- to late December. At this time there is also a marked decrease in physical contact between infants and mothers. In Ranomafana, infants attained complete locomotor independence by four months, but as early as 13.5 weeks of age (estimated from a graphical representation; Tan 2000). As predicted, the attainment of this physical developmental landmark coincided with increasing terrestriality by adults, which peaks in January in Sangasanga (11.1%) and February in Ranomafana (24.1%; Tan 2000), and is likely related to the eruption of bamboo shoots from the ground. This period of increased terrestriality may play a valuable role in refining P. simus infant locomotor skills.

By creating a simple diagram of conception, birth, locomotor independence, and weaning using data from *P. simus* at Ranomafana and Sangasanga some intriguing patterns

emerge (Fig. 6). It appears that it is possible for *P. simus* mothers to be nursing and pregnant concurrently. In Sangasanga, concurrent lactation and pregnancy has occurred with some individuals nursing an estimated 25 days into their subsequent pregnancy. This is also supported by average duration of reproductive phases in captivity (Roullet 2012).

Concurrent pregnancy and lactation has been observed in other social primates such as humans (Merchant *et al.* 1990), macaques (Tanaka *et al.* 1993), and marmosets (Saltzman and Abbott 2005). Although not explicitly stated, it may also occur in *Propithecus verreauxi verreauxi* (see Lewis and Kappeler 2005). It has been suggested that macaques wean their current infant once the developing fetus survives the greatest at-risk period for abortion, which is during the first month of pregnancy (Tanaka *et al.* 1993). This may also hold true for *P. simus*.

Mortality

Infant mortality rates at Sangasanga were higher than those reported from Ranomafana where mothers successfully reared all their infants during the study period (n = 9; Tan 2000). Over the duration of the study at Sangasanga infant mortality was nearly 50%, which was similar to mortality rates for ring-tailed lemurs and sifakas (Gould *et al.* 2003; Richard *et al.* 2002). There is no evidence of infanticide.

In Sangasanga, half of all infant deaths occurred in December and January. This may be related to increasing independence of infants from their mothers that leaves the infants more vulnerable to predation. Threats of predators and intragroup aggression have been proposed to be highly influential in the rate of infants attaining independence (Förster and Cords 2002), which may also explain the acquisition of locomotor independence at nearly the same time as a peak in infant mortality rates. Additionally, in late December and early January, researcher presence decreased due to the Christmas and New Year holidays, when field hours were reduced. It is possible that researchers acted as inadvertent sentinels driving away possible predators.

As noted by Lawler (2011) in an overview of demographic concepts, the population growth rate in the majority of primate species is mostly affected by adult survival, with populations being more resilient to losses of immature individuals. Mortality rates for greater bamboo lemur males could not be estimated due to their frequent movement between

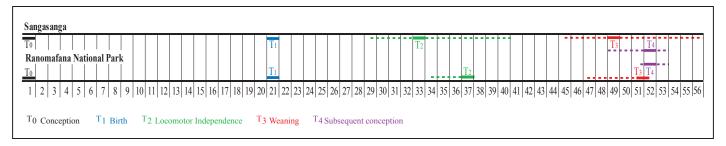


Figure 6. Scaled timeline of *P. simus* female reproductive cycle and infant developmental landmarks. Dotted lines cover the range of observed values from Sangasanga with solid bars over the average week. Dotted lines for Ranomafana reflect ranges noted in Figure 5.4 of Tan (2000) with bars over values reported in that text.

groups and possibly to groups outside the study area. Only males who died while wearing active radio collars within the study area were recovered. One such set of remains indicated predation by fossa (*Cryptoprocta ferox*). Predation of *P. simus* by raptors was reported in Ranomafana (Wright *et al.* 2012), and is suspected to occur at Sangasanga. At Sangasanga, the lemurs become highly agitated in the presence of these large birds, but an attack has never been witnessed.

It was possible to estimate female adult mortality, which was highest in group West 1 who lost half its breeding females (two of four) in 2013. The females were predated on during the same time period, in August, and both sets of remains were recovered, but the predator could not be identified due to the state of decomposition. All presumed natural deaths in the monitored groups occurred during the dry season, while the only known poaching event occurred at the beginning of the rainy season in West 2, and resulted in the loss of a breeding female and her infant. This incident coincided with the extraction of bamboo to make baskets to transport the litchi harvest to market, supporting the conclusion that most bushmeat collection in Madagascar is from opportunistic hunting while collecting non-meat forest products (Gardner and Davies 2013), but see Golden (2009).

Despite an infant mortality rate of nearly 50%, the population of P. simus in Sangasanga increased, with an overall growth rate of 19.0% from 2011 to 2014 in the focal groups. All groups monitored experienced growth in 2013, but with only East 1 and 2 continuing to expand through 2014. West 1 has not rebounded since the aforementioned precipitous decline in the number of its breeding females due to natural causes. West 2 also experienced faltering numbers due to the loss of one of its breeding females to a poacher. Since immigration of females into groups has not been observed in this study, it is predicted that these groups will not recover their numbers of breeding females until the two surviving infant females from 2013 reach sexual maturity. However, migration of females was seen for the first time after more than a decade of monitoring in Ranomafana, at a time when the population was plummeting (Wright et al. 2012).

These data shed light on intraspecific variation in greater bamboo lemurs at two sites with divergent disturbance regimes and ecological profiles. Flexibility in reproductive cycles as seen in the shift of the birth pulse as well as interindividual variation in infant development may promote resilience in unpredictable environments. Infant mortality rates vary greatly between sites, but additional long-term information is needed as this can affect the ability of groups to rebound after a population decline. The identification of intraspecific differences highlighted here underscores the need for expanded long-term investigations at sites with differing selection pressures throughout the geographic range of greater bamboo lemurs. These data will be useful for population viability analyses, predicting resilience to hunting pressure and habitat loss, and for the development of conservation strategies.

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Assessing the Population Status of the Critically Endangered Niger Delta Red Colobus (*Piliocolobus epieni*)

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Abstract: A survey to assess the conservation status of the Niger Delta red colobus (*Piliocolobus epieni*) was carried out across the species' range in central Niger Delta in 2013. The survey results suggest that the population has declined significantly since it was first assessed in 1996; c. 90% lower than the previous estimate of <10,000 individuals about 20 years ago. Using cumulative observation data, I suggest that the current estimate of the total population surviving in the wild can only number in the hundreds rather than the thousands. The major threats are habitat loss and degradation, but hunting is still a significant threat to the species' survival. Based on spatial analysis of forest cover within the species range over a 22-year period, it is estimated that deforestation occurs at an average of 1.2% annually, thus, suggesting that if the species' decline is primarily driven by habitat loss, it may become extinct in 5 years or less. Only two areas were found where viable populations of the species still persist. The forests in these areas are severely fragmented, but together total approximately 78 km². With no formal protection throughout its range, priorities for conserving remnant populations of the species must include the establishment of effective conservation areas, taking into consideration the needs and livelihoods of local communities, and promulgating laws and policies (both at government and local levels) that fully protect the species throughout its range.

Key Words: Niger Delta, *Piliocolobus epieni*, habitat, population, distribution, red colobus

Introduction

The Niger Delta red colobus Piliocolobus epieni (Grubb and Powell, 1999) became known to science in 1993 in the course of wide-ranging wildlife inventory and mapping surveys across the Niger Delta undertaken by the late C. B. Powell (Powell 1993). His unexpected discovery of this primate, supported by the skin of a specimen provided by a native of Gbanraun (in present-day Bayelsa State) (Oates 1994), drew the interest of international primatologists and conservationists. At the time, the monkey was believed to be a close relative of one of the geographically closest red colobus populations-either Preuss's red colobus (Procolobus preussi), over 150 miles away along the Nigerian-Cameroon border or of the Bioko red colobus (Procolobus pennantii pennantii)—and as such was believed to be a subspecies of Procolobus badius (sensu lato) in the pennantii group (Werre and Powell 1997). In subsequent years, further studies of vocalizations and mitochondrial DNA by Ting (2008) suggested that epieni was not closely related to either, and it was consequently considered a distinct species, Procolobus epieni.

Groves (2001, 2007) placed most of the different forms of red colobus, including *epieni*, *pennantii* and *preussi*, as separate species all in the genus *Piliocolobus*.

Prior to this survey, there has been only one range-wide study of this monkey. The study by Werre (2000), between 1994 and 1997, established that P. epieni occurs only in the Niger Delta's freshwater swamp forest, often referred to as marsh forest, which has a year-round, high water table but does not suffer deep flooding or tidal effects (Oates and Werre 2009). The study indicated that the more clumped distribution of food species in these forests was a key factor restricting the monkey to its limited range of about 1,500 km², demarcated by the Forcados River and Bomadi Creek in the northwest, the Sagbama, Osiama and Apoi creeks in the east, and the mangrove belt to the south (Oates and Werre 2009) in the central Niger Delta, Bayelsa State, Nigeria. The Niger Delta red colobus has the most restricted range of any of the Nigerian monkeys (Blench 2007). Reports from local hunters indicated that it was common over much of its range at the time it was first discovered (Powell 1993), and was thought to be in no immediate danger. Conservation scientists soon realized, however, that the species was gravely threatened, particularly from habitat loss and degradation (see Werre and Powell 1997). Werre (2000) estimated that the total population of *P. epieni* had fallen below 10,000 individuals (Oates 2011), and the status of the species has deteriorated further since then. By the early 2000s, uprisings and conflicts over petroleum and land and human rights had erupted in the Niger Delta, hindering research and conservation activities in the region.

The Niger Delta faces a peculiar combination of social, economic, environmental and political challenges. The largest river delta in Africa, the region supports the second largest swamp forest on the continent and the third largest contiguous mangrove forest in the world. It has played an important role in the Nigerian and global economy since 1600 (Blench 2007). Crude oil in all its forms, from extraction to production, symbolizes the Niger River Delta of today and is the catalyst for major social and political tensions in the region. It is infamous as the chief cause of devastating environmental pollution and forest degradation since the late 1950s when oil was first discovered in the Oloibiri community of Bayelsa State. Road and canal construction have affected especially areas that can be considered as prime habitat for red colobus. Drilling in the Niger Delta opened up the forests for commercial logging and the bushmeat trade (Werre and Powell 1997; Blench 2007; Oates and Werre 2008; Oates 2011), resulting in the loss of important colobus food trees—especially Hallea ledermannii (Rubiaceae), locally called abura, being felled at a high rate by artisanal loggers (Oates and Werre 2008). Abura has been the most important timber species after Triplochiton scleroxylon (Malvaceae) since 1949, and by 1951 export volume had increased more than five times (Blench 2007). Most of the Abura came from the swamp forest between the Nigerian Lowland Forests ecoregion westwards bordering the delta. This source was soon depleted and loggers started to focus more on the delta, where exploitation was at the same time facilitated by increasing oil exploration (Blench 2007). With the national population growth rate at about 3% per annum, the oil industry continues to attract a huge number of migrant job seekers from across Nigeria and internationally, markedly increasing the human population in the delta, now estimated to be over 30 million people with a significant portion living in Port Harcourt, Rivers State (Nigeria National Population Commission Database 2006), about 86 km as the crow flies from Yenagoa, the Bayelsa State capital. These two growing cities are the major commercial centers for the delta's forest resources. A rapidly growing human population depleted commercial fish populations in the delta's rivers (see Blench 2007), which increased the rate of bushmeat hunting in the region.

Due to an assumed major decline in the species' population over the last 30 years and continued pressure from hunting and habitat loss, the Niger Delta red colobus is classified as Critically Endangered on the IUCN Red List (as *Procolobus pennantii epieni*; Oates and Struhsaker 2008), and has been listed as one of the world's 25 most endangered primates (Oates and Werre 2009). The goal of the survey was to gather

information to determine the status of remnant populations of *P. epieni* across its range—data that can be used to develop a conservation action plan. I also endeavored to map the current distribution of the red colobus in relation to habitat conditions and threats affecting *P. epieni* (type, distribution, and intensity), in order to identify priority areas for its conservation.

Methods

Survey sites

Werre (2000) indicated 16 communities (forests) where he saw or heard P. epieni or obtained reports of its presence from hunters: *1Sampou, Azama, *Gbanraun, *Norgbene, Ogboinbiri, Keme-Ebiama, Kokologbene, Ukubie, Egbemo-Angalabiri, Ogbotobo, Lalagbene, Adi-Egbe, Adagbabiri, Eriama, Toru-Ebeni and Bolou-Orua. He visited three other areas—Bomadi, Orobiri and Olota—but there were no reports of red colobus occurring there. Our study sites included all the communities listed in Werre's (2000) report as well as a number of other locations suggested by hunters. The area delineated in Figure 1 (shaded grey) as the range of *P. epieni* is within the present-day Bayelsa State. The 16 communities that were important for the survey are located mostly in Ekeremor, Sagbama and Southern Ijaw Local Government Areas. The range of *P. epieni* according to Werre (2000) is within geographic coordinates 5.31'E and 4.06'E at its northern and southern limits and 5.38'N and 6.27'N at the western and eastern extent. The town of Bomadi (in Delta State) is at the northernmost tip of the species' range, while Sagbama, Ajamabiri and Lobia are located at the eastern, western and southernmost edges of its distribution, respectively. The range of P. epieni overlaps areas covered by both the Niger Delta swamp forest and the Central African Mangrove Ecoregions; significantly, much of the range is within the swamp forest zone in the central and eastern parts.

The red colobus range is generally low-lying; between 31 m below and 42 m above sea level. Average altitude in this region is 17 m (DIVA-GIS²). One of the most significant features of the Niger River Delta is the hydrology and drainage; the region has an elaborate network of coastal waterways and winding tributaries of the River Niger. Piliocolobus epieni occurs mostly in the western central part of this region, an area described by Powell (1993) as the 'marsh forest' zone —freshwater tidal sector, with permanently water-logged ground that does not receive much of the annual Niger flood (Werre and Powell 1997). The major changes in the hydrological regime come from the Atlantic Ocean's tides and the Niger River flood, which begins toward the end of the rainy season in August, peaks in October, and tapers off in December (Blench 2007). Some parts of the species' range are also within the band of mangrove forest close to the Atlantic. In

¹ Areas with an asterisk are locations where Werre (2000) saw or heard *P. epieni*.

² DIVA-GIS is a free computer program for mapping and geographic data analysis. Website: http://www.diva-gis.org>.

front of the mangrove belt and close to the sea are ephemeral coastal barrier islands often covered in transitional vegetation (Blench 2007).

The delta region has one of the highest mean annual rainfalls in tropical Africa. Given the proximity of the region to the coast, precipitation is very high, receiving rain throughout the year but mostly from March through to October, with

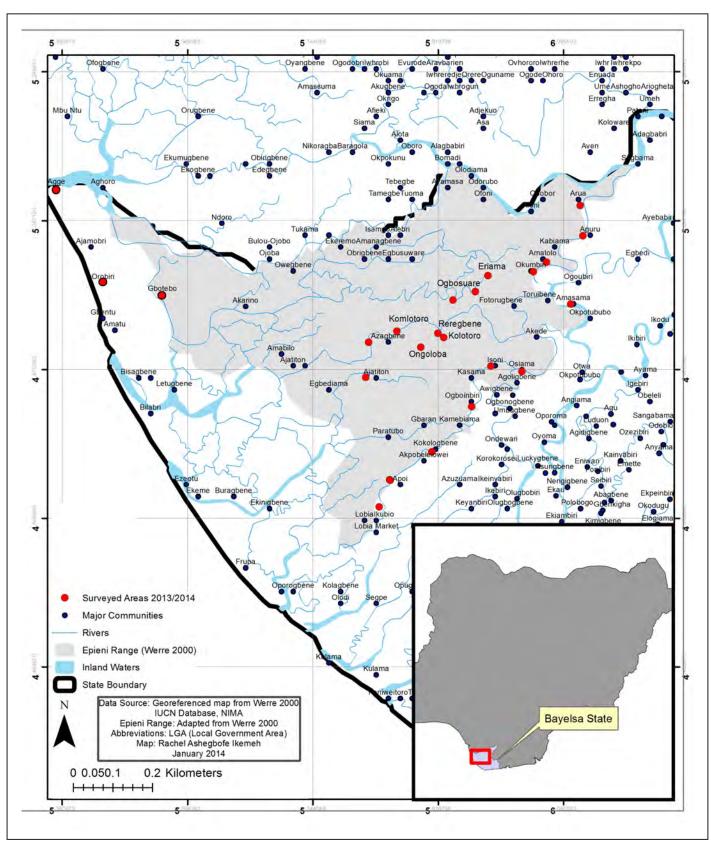


Figure 1. Areas in the Niger Delta surveyed in 2013–2014.

intermittent showers during the other months. According to Blench (2007), mean annual rainfall averages 4,000 mm in areas close to the coast around the species distribution region. Even during the dry season, from January to February, mean monthly rainfall is 150 mm in the delta (Blench 2007). DIVA GIS estimates a mean annual minimum and maximum temperature for the areas where *P. epieni* is found as 22°C and 30°C, respectively.

Survey methods

Our survey focused on areas where natural forests remain and in designated forest reserves indicated on the map within the range of *P. epieni*. Field surveys were generally exploratory, with visits to forests close to the aforementioned locations but also visiting other forest areas when receiving new and reliable information from indigenous people. The swamp forests where *P. epieni* occurs is not easily accessible on foot. During the dry season we were able to carry out surveys following available trails used by hunters and other people. When water levels were too high for us to wade through, surveys were conducted using dug-out canoes along canals created and used by local people.

Encounters with *P. epieni* (sightings and vocalizations) were recorded using the format recommended by White and Edwards (2000)—the generic name of the location, GPS coordinates (waypoint and in the field notes using a Garmin GPS 62s), date, time and type of observation, approximate number of individuals observed, activity and behaviors, and habitat type/condition. All evidence/identifications of other primates and large mammals were also recorded, as well as

evidence of human activities. Habitat data were assessed prior to field visits using remote sensing images, and our field surveys provided opportunities for ground-truthing and assessing habitat status.

Data collection was carried out from 14 April to 26 August, 2013. Field surveys were carried out from 07:00 to 12:00 and 16:30 to 18:00; times when the colobus monkeys are most active. We tried to adhere strictly to these time schedules, but sometimes the survey trails were too far from our camp (insecure areas or flooding meant that on some occasions we had to stay in villages some distance from the trails).

Since one of the primary aims of the survey was to determine the population status of P. epieni across its range in the central Niger Delta, interviews made up an integral part of our research. Werre (2000) also used a combination of systematic reconnaissance, direct searches, and interviews. Local people were interviewed for information on P. epieni populations and asked how they interacted with the species in their respective communities (n = 21; Table 2). Only open-ended questions were used.

Overall, we travelled about 589 km in and around the species' range; 183 km of which were covered on foot in systematic field surveys, and 54 km were surveyed from locally constructed dug-out canoes in shallow creeks/canals where it was not feasible to walk. The rest of the distance travelled was in motor boats or trucks when moving between communities. Figure 2 shows the survey locations and systematic sampling routes.

Table 1. Summary of field observations of Piliocolobus epieni.

Locality (major com- munities or camps nearby)	Forest surveyed (km²)¹	Encoun- ter rate/ km ^[2]	Type of observation	No. of individuals counted ³	Other primates seen with <i>P. epieni</i>	Other communities using the forests visited	Notes
Otolo (camp of Kunu Community)	11.8	0.12	Sighting	>25	Putty-nosed, white- throated monkeys, olive colobus	Ogbosuare, Adagbabiri, Eriama, Sampou	Observed troop for 20 minutes before our presence was detected.
Sampou	15.4	0.29	Calls	Unknown	Possibly mona and putty-nosed monkeys	Azama, Kunu	Very Distant
Ongoloba (camp of Azagbene community)	12.6	0.44	Sighting, calls	<30	Putty-nosed monkey, mona monkey	Kolotoro, Reregbene	-
Kolotoro (camp of Aleibiri community)	6.6	0.26	Calls	±70	Putty-nosed, mona, and white-throated monkeys	Ongoloba, Azama, Reregbene, Ogbosuare	Dense tree cover hindered direct observation.
Apoi	10.9	0.07	Sighting	≥40	Putty-nosed monkey, red-capped mangabey	Gbanraun, Kokolog- bene, Ukubie	Group watched for 15 minutes
Egbemo-Angalabiri	22.8	0.42	Sighting	≥15	Putty-nosed, mona, and white-throated monkeys, olive colobus	Azagbene, Komlotoro	-
Bolou-Orua	27.3	0.03	Calls	Unknown	White-throated monkey	Toru-Orua (northwest), Kaebiama (south), Agoro (east)	The only record for this site. Identity uncertain because the sound was very distant.

¹ Size of forest area is calculated from USGS Landsat Satellite imagery of 2013. This size is only an approximate measurement and should not be construed as the true size of the forests. It should also be noted that we have attempted to use names of communities using a particular forest area but it does not suggest the ownership of a forest area or is conclusive of all communities entitled to that forest area.

² Encounter rate was calculated using the sum of observations/total distance surveyed in each site.

³ Number of individuals indicated on the table is not an absolute figure of the number of individuals present in the group but was estimated based on point counts from the observer's angle of view, guess-estimate from group size appearance and suggestions from the sound of activity and/or shaking on forest branches.

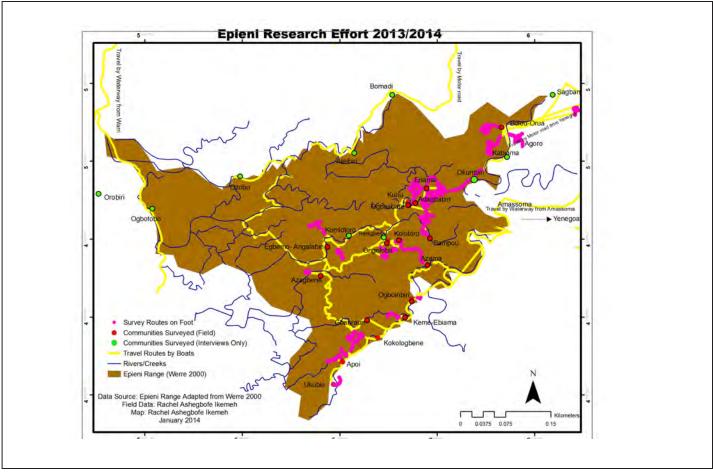


Figure 2. Communities and survey transects.

Table 2. Comparison of two surveys in Piliocolobus epieni status across different communities.

Site	Communities with P. epieni (Werre 2000)	Extinct (reports and field surveys 2013)	Present (confirmed from field surveys 2013)	Local reports	Comments
1.	Sampou*	-	Yes	No	Interviews were not conducted in this community.
2.	Azama	-	No	Yes	Possible since it shares forests with Kolotoro.and Sampou.
3.	Gbanraun*	-	Yes	Yes	Although we did not see any colobus in the Gbanraun part of the forest, observations from Apoi suggest grousp may travel through the forest cluster shared by both communities where boundaries cannot readily be determined.
4.	Norgbene*	-	No	Yes	Forests surveyed from adjoining Egbemo-Angalabiri but no colobus were observed although a group was recently seen by a hunter in the forests close to the community.
5.	Ogboinbiri	Yes	No	No	-
6.	Keme-Ebiama	Yes	No	No	-
7.	Kokologbene	-	Yes	Yes	Same reason as for Gbanraun.
8.	Ukubie	Yes	No	No	-
9.	Egbemo-Angalabiri	-	Yes	Yes	-
10.	Ogbotobo	Possible	No	Uncertain	Hunters in this community say they have not seen or heard colobus in the last 3 years and are not sure if still present.
11.	Lalagbene	Yes	No	-	-
12.	Adi-Egbe	Yes	No	-	-
13,	Adagbabiri	Yes	No	-	-
14,	Eriama	Yes	No	No	-
15,	Toru-Ebeni	Yes	-	-	-
16.	Bolou-Orua	Possible	Uncertain	No	-

^{*}Areas where Werre (2000) saw P. epieni.

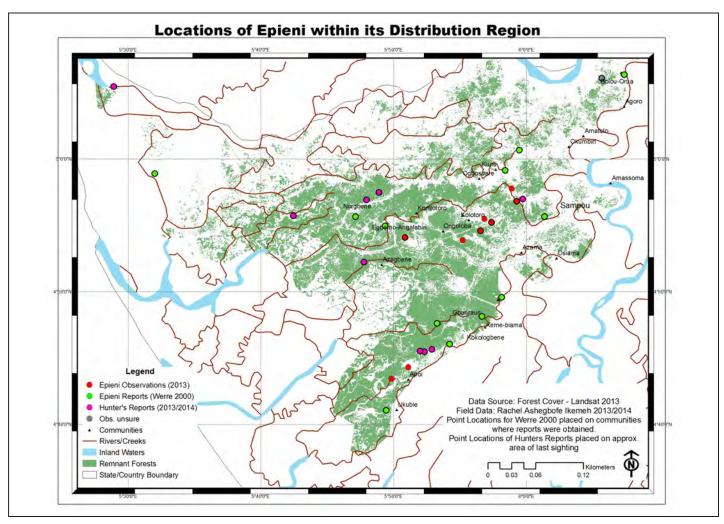


Figure 3. Locations of P. epieni observed during this survey and associated reports.

Results

This survey established the continued presence of the Niger Delta red colobus in some parts of its presumed range, specifically in the forests east of the communities of Kunu and Adagbabiri, around the Otolo camp, in the Sampou forest area, less than 2 km from the Kunu forests, in Ongoloba (a camp village of the Azagbene community, in Kolotoro), and another village of the Aleibiri community about 5 km from Ongoloba. *Piliocolobus epieni* was observed in Egbemo-Angalabiri, where the forest is contiguous with the Ongoloba (Azagbene) community forests. *Piliocolobus epieni* was also seen in a relatively large group in the Apoi forests, adjacent to the community forests of Gbanraun and Kokologbene. The record at Bolou-Orua was based on very distant vocalizations and was not absolutely certain. Figure 3 shows the locations of these records.

The occurrence of the Niger Delta red colobus is largely concentrated in two contiguous forest patches, combined covering about 7,896 ha. The first forest cluster covered more than 4,368 ha, extending east from Kunu connecting to forests in Sampou, and then south to Kolotoro and Ongoloba, terminating at the eastern flank of Egbemo-Angalabiri and

north of Azagbene. A smaller cluster of about 2,587 ha where the species was relatively common was made up of forest patches from Kokologbene extending west to Gbanraun and southwards to Apoi, terminating at the fringes of forest close to Ukubie.

In the 1990s, visitors to the forests near the town of Gbanraun observed *P. epieni* relatively easily (Oates 1994). During our surveys, however, we failed to find the colobus over two full days of travel in c. 500 ha of forests where the species had previously been intensively studied and viewed by several scientists and conservationists. This suggests that the population there had undergone a severe decline. Werre (2000) estimated that the entire population of P. epieni may have fallen below 10,000 individuals. Based on cumulative observations made of c. 200 individuals (see Table 1) during this survey, I suggest that the current population size may now number in the hundreds rather than the thousands. The actual population estimate may be somewhat higher if, for example, the survey effort and area covered were insufficient, and group sizes were poorly counted and significantly larger, and of course if there is a significant population that neither Werre (2000) nor I are aware of. Further surveys are needed. It is evident under any circumstances, however, that the species

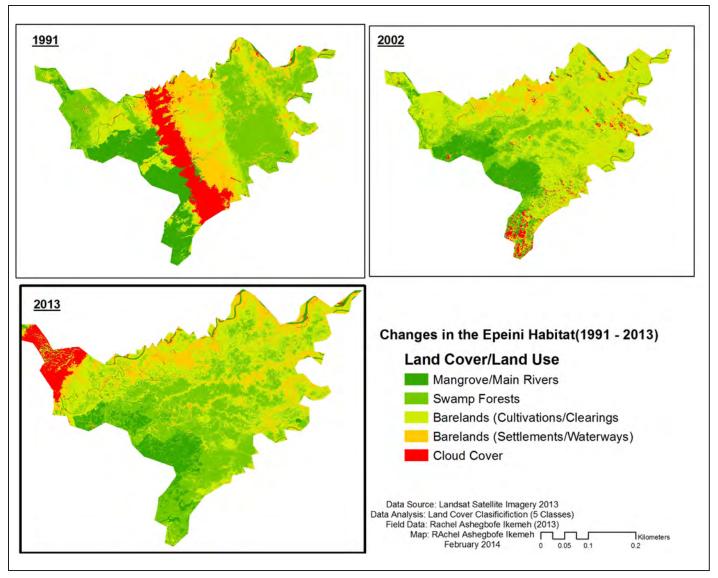


Figure 4. Changes in forest landscape within the range of P. epieni.

has been extirpated from much of its range (see Table 2), and even in localities where they had been previously reported present by Werre (2000).

Besides hunting, a major factor that has affected the populations of this species is the degree of habitat loss and degradation over the last 3–5 years. Observations on logging, occurring year-round in the species' habitat, indicate the loss of important food trees over time. By carrying out spatial analysis of available United State Geological Survey (USGS) satellite imagery (Fig. 4) it was possible to assess the rate of deforestation over the last 22 years. The results indicate that 47% of forests was lost between 1991 and 2002, and a further 12.8% of forest cover was lost during the subsequent 11 years from 2002 to 2013. The lower rate during the second period can be attributed to the civil unrest that engulfed the region at this time which dampened activities. Overall, this spatial analysis shows that there is an annual deforestation rate of about 1.2%, equivalent to about 2,200 ha (22 km²) lost annually.

Discussion and Recommendations

The historical and current range of the species still need further investigation. New and reliable reports of P. epieni in the Agge community (Delta State) presents possibilities that the species may occur in the forests of the Delta State northwards, reaching the Forcados and Burutu communities. There were also reports of a monkey that had not been seen for almost 20 years from the Emago-Kugbo community at the border of the Rivers and Bayelsa states in the Edumanom Forest Reserve. This might have been P. epieni or another undiscovered monkey. It does, however, warrant investigation, suggesting as it does that the range of P. epieni may have extended beyond the limits described by Werre (2000). Presently, the species appears to be concentrated in the central south-eastern region of the range highlighted by Werre (2000), in severely degraded and fragmented habitat totaling about 78 km².

Threats

Deforestation and habitat degradation resulting from excessive logging are the most significant that this species is facing. The number of signs of logging was six times (84% of total observations of threats identified) more than any other observed human activities considered to constitute a threat to red colobus in the region. Most forests surveyed lacked large trees and even medium-sized trees were very hard to find. Even trees not regarded as providing economically-valuable timber products were being cut down. In the north of the species' range, the forest is mostly dry or has areas where there are navigable waterways, and most trees were being cut into planks inside the forest (creating considerably more disturbance than regular logging) before being transported by tractor (in the dry season) and/or on foot (in the wet season). In the south of the species' range, trees are floated out of the forests as logs along canals dug out to connect to larger canals or creeks where the timber can be picked up by large boats and transported to major urban centers. Due to excessive logging, large trees and even medium-sized to small trees important as food sources for red colobus and other wildlife were very scarce. Satellite images analyzed for the species range show a significant loss of forest cover of 2,200 ha each year since 2002. Only in the forests of Eriama and neighboring areas did we observe large 'bush mango' trees Irvingia gabonensis. They are locally protected from logging because their seeds are commercially valuable as a soup condiment. They are gathered during the fruiting season between April and July every year and sold in large urban markets for reasonable profits.

The Niger Delta has large reserves of crude oil and gas, and extraction of these highly valuable resources has direct impacts that include deforestation for the construction of roads, drilling, and the construction of platforms and pipelines. Where access by land is difficult, as is the case in much of the range of *P. epieni*, canals are opened up and expanded, altering the hydrological regime of the ecosystems. These canals serve as waterways for motorized boats and allow for the installation of pipelines and other activities related to drilling and the transport of the crude oil. However, although oil extractive activities compromise the ecosystems, it is the indirect impact of these activities that is most devastating and large-scale. The infrastructure required to support petroleum extraction (roads, power lines, and towns) facilitates further human expansion into formerly unoccupied areas. This increased accessibility to remote areas by way of new oil roads and pipeline routes is the primary cause of excessive logging leading to severe deforestation, agricultural development, and the unsustainable harvest of wild animals as bushmeat. Another consequence of petroleum extraction (whether by bunkering [theft] or by corporate activities) is oil spillage that pollutes the riparian habitats so important for the survival of both people and the wild fauna and flora. Bunkering was on the rise in many parts of the areas surveyed, and this illegal activity raises new concerns on how to regulate oil spillage and avoid the environmentally destructive consequences of

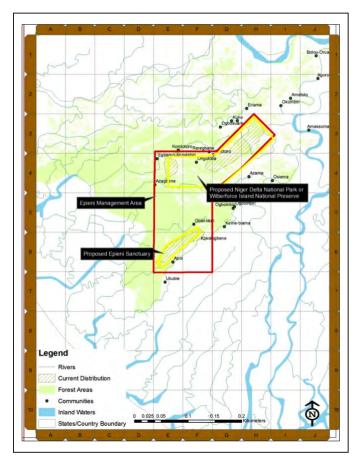


Figure 5. Proposed areas for conservation and suggested management regimes.

oil spills. Records show that 50% of oil spills are due to corrosion of poorly maintained pipelines, 28% from bunkering, and 21% from oil production operations (Nigeria, Federal Ministry of the Environment 2012).

Results from this survey indicate that hunting of colobus is very rare and almost non-existent in many areas surveyed, and the predominant threats come from logging and other socio-economic activities. Although it seems that levels of hunting correspond with the occurrence of wildlife found in the area, it can be described as opportunistic, as most of the people observed or reported to be hunting are fully engaged in either logging or fishing.

Conservation

The Niger Delta landscape is high in biological endemism and has other, also threatened, primate populations such as the endemic Sclater's guenon (*Cercopithecus sclateri*), the Nigerian white-throated guenon (*Cercopithecus erythrogaster pococki*), the red-capped mangabey (*Cercocebus torquatus*) and the endangered Nigeria—Cameroon chimpanzee (*Pan troglodytes ellioti*). There are no effectively protected areas. Without effective conservation and management of its unique species and habitat, the Niger Delta may have already witnessed the extinction of one of its endemic mammals—Heslop's pygmy hippopotamus (*Hexaprotodon liberiensis heslopi*)—and now only time and proactive measures will determine if the Niger Delta red colobus will avoid extinction.

The numbers of red colobus are now dangerously low as their habitat continues to shrink. Urgent steps need to be taken to manage the remnant population(s) and ensure recovery from their present unsustainable levels. Since the forests of P. epieni are productive for timber, crude oil reserves, and other economically important resources, it is important that specific areas be delimited, created and managed as IUCN category IV protected areas—sites where active management interventions are undertaken so as to ensure maintenance of habitats and/or to meet the requirements of a particular species, and also where certain activities are prohibited (IUCN 1994). For P. epieni, we propose that certain areas of the Otolo-Kolotoro-Ongoloba axis (140 km²) be demarcated as a national park, while the Ukubie-Apoi-Gbanraun-Kokologbene axis (21.5 km²) be protected as a conservation sanctuary (Fig., 5). These two sites are extremely important for the continued survival of this species.

The creation, management and effectiveness of these protected areas will depend of course on the full involvement of the local communities in and surrounding them, taking into consideration their well-being and livelihoods.

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Habitat Use by White-thighed Colobus in the Kikélé Sacred Forest: Activity Budget, Feeding Ecology and Selection of Sleeping Trees

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Abstract: Understanding habitat preference and use is an important aspect of primate ecology, and is essential for setting conservation strategies. This study examined the activity budget, feeding ecology and selection of sleeping trees of a population of white-thighed colobus (*Colobus vellerosus*). A group of 18 was followed during 72 days over a full annual cycle in the Kikélé Sacred Forest of the Bassila administrative region in central Benin (West Africa). Activity budget and diet were determined using scan sampling. The structure of the habitat and the physical characteristics of sleeping trees were determined using plot surveys. Resting, feeding, moving, social interactions and other activities accounted for 56.6%, 26.3%, 13.0%, 3.3%, and 0.7% of the activity budget, respectively. The group spent more time feeding and less time moving in the dry season compared to the rainy season. The diet was composed of 35 plant species belonging to 16 families, with items including leaves, fruits, seeds, buds, bark, flowers, gum, and inflorescences. Only three tree species were used as sleeping trees: *Celtis integrifolia*, *Cola cordifolia*, and *Holoptelea grandis*. Our findings suggest that the monkeys prefer tall (22.53 \pm SD 3.76 m) and large-trunked (112.07 \pm SD 14.23 cm) sleeping trees. The results of this study can be used for sound management of the white-thighed colobus in the study area and elsewhere.

Key Words: activity budget, feeding ecology, sleeping trees, Colobus vellerosus, conservation, West Africa

Introduction

Crucial components of an animal's habitat are the provision of food and resting sites that are safe from predators (Gautier-Hion et al. 1983). Activity budgets are reliable indicators of the coping strategies of primates in their environment, and are often related to the ways animals conserve energy (Milton 1998). Activity budgets are influenced by factors such as group size and habitat quality (Teichroeb et al. 2003; Wong et al. 2006). With their folivorous diet, colobines tend to reduce energy expenditure by spending long periods of time resting (Irwin 2008a, 2008b; Korstjens et al. 2010). As leaves are superabundant and widely dispersed, it is supposed that folivorous primates such as colobines do not experience intragroup scramble competition for food (for example, Colobus guereza: Fashing 2001; Procolobus rufomitratus: Snaith 2008; Colobus vellerosus: Saj and Sicotte 2007; Teichroeb and Sicotte 2009). This has also been found in Asian colobines (Yeager and Kirkpatrick 1998; Yeager and Kool

2000). For this reason colobine monkeys would be expected to form large groups, which is not always the case. This is the "folivore paradox" (Steenbeek and van Schaik 2001; Snaith 2008).

The colobine diet varies in species composition with the food resources available and the floristic composition of their habitats. Colobine monkeys also eat fruits and other plant parts besides leaves (for example, *Procolobus verus*: Oates 1988, Davies *et al.* 1999; *Colobus polykomos*: Dasilva 1994, Davies *et al.* 1999; *Procolobus badius*: Davies *et al.* 1999; *Colobus vellerosus*: Teichroeb *et al.* 2003).

Sleeping sites (nests of leaves, holes in trees, or the branches of trees) are night refuges for diurnal animals, and affect habitat use. The study of sleeping sites, therefore, may help to understand some aspects of their behavior. The choice of sleeping sites by animals is influenced by predation avoidance and access to food (Albert *et al.* 2011; Holmes *et al.* 2011; Teichroeb *et al.* 2012), thermoregulation (Fan and Jiang 2008), and social factors (Anderson 1998). The white-thighed

colobus (*Colobus vellerosus*) is endemic to West Africa and is listed as Vulnerable on the IUCN Red List (Oates *et al.* 2008). Despite conservation efforts in Côte d'Ivoire, which covers a significant part of its range, the conservation status of *C. vellerosus* is deteriorating, and the species may now be Endangered (Gonedelé Bi *et al.* 2010). Most of the behavioral studies on *C. vellerosus* have been conducted in Ghana. According to Wong *et al.* (2006), its diet is dominated by leaves (79%), but also comprise fruits (10.7%), flowers and buds (6%), seedpods (4%) and sap (0.3%). Wong and Sicotte (2007) found that the activity budget of *C. vellerosus* comprises 22.0% feeding, 68.6% resting, 6.8% moving, and 2.6% social activities, and is influenced by group size and group composition as well as food availability (Teichroeb *et al.* 2003).

Habitat types, plant communities and seasonal variation in resource availability influence diet composition. In Benin, *C. vellerosus* is restricted to the Guineo-congolese zone and Guineo-sudanian zone (Djègo-Djossou and Sinsin 2009). The species is legally protected in forest reserves (Djègo-Djossou, 2013) whereas in the Kikélé Sacred Forest its protection is based on traditional beliefs (Djègo-Djossou *et al.* 2012). The studies mentioned above were conducted in typical Guinea-Congo semi-deciduous forests, and here we report for the first time on the activity budget, food resources and dietary composition, as well as the physical characteristics of the trees selected as sleeping sites, of *C. vellerosus* in a dry forest in the Kikélé Sacred Forest.

Methods

Study site

The Kikélé Sacred Forest (13 ha) is in the Bassila administrative region near the village of Kikélé in central Benin, West Africa (Fig. 1). This forest is occupied by a single, multi-male/multi-female group of *Colobus vellerosus* of 18 individuals that has been protected by traditional beliefs for decades (Djègo-Djossou *et al.* 2012). The Sacred Forest is extended by a gallery forest that surrounds the entire village and is fragmented by agricultural clearings and access roads.

The climate of Kikélé is of the Sudanian dry type, characterized by a dry season from mid-October to mid-April, alternating with a rainy season from mid-April to mid-October. Although the climate is dry, yearly rainfall (1300 mm) is higher compared to other regions in Benin (950-1200 mm). The vegetation of this Sacred Forest contains tall trees that are typical of semi-deciduous forests. There are several vegetation types: dense forest, woodland, and savanna. The most common species in this region are similar to those of the Boabeng-Fiema Monkey Sanctuary, Ghana. They include Cola gigantea (Sterculiaceae), Celtis zenkeri and C. toka (Ulmaceae), Antiaris toxicaria (Moraceae), Holoptelea grandis (Ulmaceae), Erythrophleum suaveolens (Leguminosae - Caesalpinioideae), and *Khaya grandifoliola* (Meliaceae) (Adomou 2005). Besides C. vellerosus, the mammal fauna of the Kikélé Sacred Forest comprises a few individuals of

Cercopithecus mona and various rodents, including the rare Beecroft's flying squirrel Anomalurus beecrofti.

Data collection: Activity budget and food resources

Data were collected using instantaneous scan sampling (Altmann 1974) during an annual cycle from February 2010 to January 2011. In optimal conditions, the scans were made every 30 minutes from 6:30 am to 6:30–7:00 pm when the monkeys would retire to a sleeping tree. Observations were made twice a month during three consecutive days with an interval of at least seven days between each observation period. During each scan, data were registered for five minutes on the first five adult or sub-adult monkeys seen clearly (Arroyo-Rodriguez *et al.* 2007). A total of 1,772 scans were made over 886 hours of observations. Activities recorded were grouped into five categories: social interactions, resting, moving, feeding and other (auto-grooming, vocalization, scratching, urination). When feeding, the plant species and parts eaten were recorded.

Data collection: Habitat characteristics

Vegetation structure was determined in two forest patches—Patch 1 in the Kikélé Sacred Forest and Patch 2 a connected gallery forest—through plot surveys following Braun-Blanquet (1932). Patch 2 was visited by the monkeys only occasionally. A total of 16 plots were set up at random in

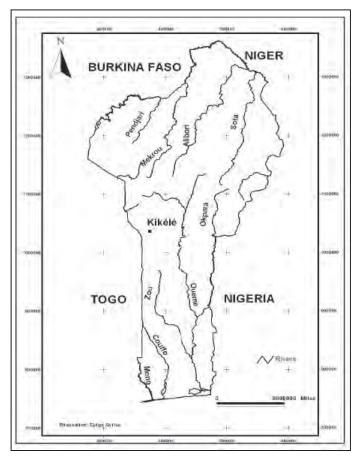


Figure 1. Map of the study site showing the location of the Kikélé Sacred Forest, Benin.

four locations over the home range of the *C. vellerosus* group: $10 \text{ square plots of } 30 \times 30 \text{ m}$ in Patch 1 (six in the dense forest, two in the woodland, and two in the savanna); and six rectangular plots of $25 \times 20 \text{ m}$ in Patch 2 (gallery forest). Plants with a diameter at breast height (DBH) of 10 cm or more were identified in each plot (Chapman *et al.* 1992). The height and the location of each sleeping tree were also recorded.

Data analysis: Activity budget, diet and foods resources

The time spent on each activity was estimated indirectly by calculating the percentage between the number of records of the activity and the total number of records. Data were computed using Statistica 10.0 and the significance level was set for analyses $\alpha=0.05$. The three-day observation period is the unit of analysis (N = 24). An analysis of variance was performed to compare the times spent in each activity in the dry season and the wet season. The proportions of the items consumed were estimated indirectly by calculating the percentage of feeding records for each item against the total number of feeding records records.

Data analysis: habitat structure and computation of ecological indexes

Three indices were computed to assess the habitats occupied by the colobus monkeys. The Shannon-Wiener Index of Diversity was used to estimate plant species diversity. Sorensen's Coefficient (S) was calculated to compare similarity between the two forest patches: S = 2C/A + B, where C is the number of species shared in both patches; A and B the number of species specific to each patch. If $S \le 0.5$ the communities compared are dissimilar; if S > 0.5, the communities compared are similar. The Evenness Index of Pielou was used to examine how evenly the species recorded are represented in each habitat.

We also calculated the patch attendance rate through the ratio between the number of days where the colobus used Patch 1 and/or Patch 2, and the total number of observation days. We calculated the average diameter and height of sleeping trees and all the trees in each plot.

Results

Activity budgets

The time the *C. vellerosus* group spent resting was more than twice the time it spent feeding (56.6% vs. 26.3%), and more than four times the time allocated to moving (56.6% vs. 13.0%) (Fig. 2). Social interactions and other activities accounted for only 3.3% and 0.7% of the activity budget, respectively.

Activity budgets varied seasonally and monthly (Fig. 3). Seasonal fluctuations in feeding (df = 23, F = 5.02, p = 0.03) and moving (df = 23, F = 12.6, p = 0.01) were statistically significant, while those for resting, social interactions and other activities showed no difference (df = 23, F<4.28 and p > 0.05 in each case). Regardless of the month, the time spent on resting was always more than 50% of the total activities.

Daily activity pattern

The monkeys were very active in the early morning; activities were dominated by moving and feeding. Activities could be broadly categorized into three periods: (i) in the morning, between 7:00 am and 10:00 am; (ii) in the afternoon, between 12:00 am and 2:00 pm, activities were dominated by resting and social interactions (grooming, physical contacts, playing, and scratching); whereas (iii) in the afternoon and early evening, between 3:30 pm and 5:30 pm, feeding, moving and social were the predominant activities. The large majority of social interactions were affiliative (94% were grooming and playing).

Habitat characteristics

Sixty species of 28 families were recorded in Patches 1 and 2. Most of the trees were of the families Moraceae (18% of the species) and Leguminosae (13%). Although the number

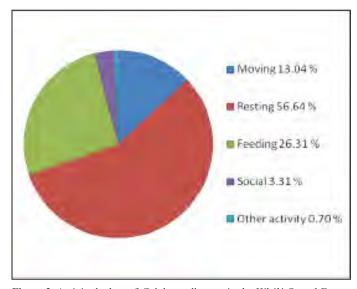


Figure 2. Activity budget of *Colobus vellerosus* in the Kikélé Sacred Forest, Benin.

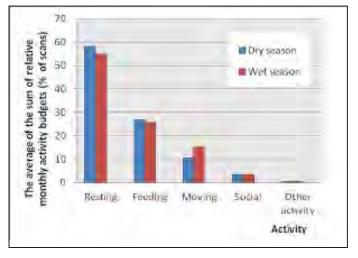


Figure 3. Seasonal variations in the activity budget of *Colobus vellerosus* in the Kikélé Sacred Forest, Benin.

of food plants was similar in the two patches, the monkey troop used the forest of Patch 1 every day and entered the gallery forest of Patch 2 on only 57% of the days. Sorensen's Index (0.33) showed a significant difference between the patches. The Evenness Index of Pielou had similar value for both patches (0.97) indicating an even distribution of recorded species (Table 1). The Shannon-Wiener Index of Diversity was also high in both patches, with its value being slightly higher in Patch 2 (H = 5.19) than in Patch 1 (H = 4.87) (Table 1).

Food plants and items consumed

The colobus monkeys ate 60 items; 59 plant parts (leaves 53.1%, fruits 33.3%, seeds 2.5%, stems 1.3%, bark 1.4%, buds 3.1%, flowers 2.45%, and petioles 2.8%) and one prey (ants). The plant parts came from 35 species belonging to 16 families (Table 2). The best represented families in the diet were the Leguminosae (29% of species) and Moraceae (23%). Leaves and fruits contributed more than 90% of the diet (Fig. 4).

Characteristics of sleeping trees

Over 72 nights, *C. vellerosus* used 13 trees of three species as sleeping sites in Patch 1. The species were *Celtis integrifolia*, *Cola cordifolia*, and *Holoptelea grandis*. The troop's favorite species was *C. integrifolia*; six trees (DBH = 90–125 cm) were used on 86% of the 72 nights. Five *H. grandis* (DBH

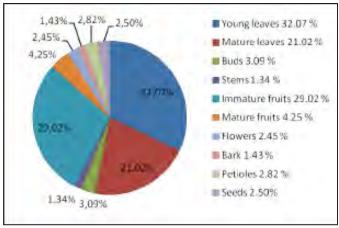


Figure 4. Annual diet of Colobus vellerosus in the Kikélé Sacred Forest, Benin.

= 100-135 cm) were used on 10%, and two *C. cordifolia* trees (DBH = 110-120 cm) were used on 4%. The frequency of use of different trees in each species varied. Two *Celtis integrifolia* trees were used more than the other four individuals. The average diameter at breast height (DBH) and mean height of the 13 sleeping trees were $112.07 \pm SD$ 14.23 cm and $22.53 \pm SD$ 13.76 m, respectively, while the averages for all trees measured were $53.72 \pm SD$ 38.26 cm for mean DBH, and $17.23 \pm SD$ 9.81 m for mean height. Of note is that a sleeping tree could be used for several consecutive nights. One sleeping tree was used for two consecutive nights on twelve occasions, three consecutive nights on two occasions, and once for four consecutive nights.

Discussion

Activity budget

Colobus vellerosus of the Kikélé Sacred Forest showed an activity pattern similar to that of most colobines, with time spent on resting much greater than that spent on feeding. Table 3 shows the activity budgets of several species of black-andwhite colobus monkeys and that of C. vellerosus in the Kikélé Sacred Forest recorded in this study. With the exception of Colobus guereza in Ituri, Democratic Republic of Congo, and C. angolensis ruwenzorii in Nyungwe, Rwanda, with 44% and 32% of the time spent on resting, respectively, all studies show that black-and-white colobus monkeys spend more than 50% of the time resting. Long resting time among colobines has been explained in a number of ways. Some authors have linked it to the need to ferment leaves for their digestion or to the quality of the habitat (Marsh 1981; Oates 1988; Korsjtens et al. 2010). It has also been considered a strategy of behavioral thermoregulation for Colobus polykomos, as it may limit energy losses (Dasilva 1992, 1994).

Differences in group activity budgets may be explained by differences in group size as social activities are more frequent in larger troops (Teichroeb *et al.* 2003), as well as by other factors such as predation risk, the social structure of troops, seasonality, and the availability and distribution of food resources (Kinnaird and O'Brien 2000). The time that *C. vellerosus* spent resting in Kikélé Sacred Forest was lower than that recorded for the same species in Ghana. This could be explained by the small size of the Kikélé group and the relatively poor quality of the habitat (Wong and Sicotte 2007). Our results contrast with the theory that indicates that time

Table 1. Habitat characteristics in the Kikélé Sacred Forest, Benin.

Designation	Habitat	Area (ha)	Floristic diversity	Potential food plants (% of spp.)	Shannon Wiener Index	Pielou Evenness Index
Patch 1 (Sacred Forest)	Dense forest	6.38	40	51%	4.87	0.97
	Woodland	2.10	16	44%	3,52	0,72
	Savanna	3.56	26	27%	3,11	0,55
Patch 2	Gallery forest	6.25	32	50%	5.19	0.97

spent resting increases when it is hotter (Chaves *et al.* 2011). We found no difference in time spent resting by colobus in dry and rainy seasons. This is probably a consequence of the degraded habitat; Kikélé Sacred Forest is a small fragmented forest.

Feeding

Fifty eight percent of the plant species occurring in the study area contribute to the diet of *Colobus vellerosus*. Our findings are congruent with previous works that suggest that the Leguminosae provides the main food sources for colobus monkeys (Davies *et al.* 1988). Consumption of *Erythrophleum suaveolens* leaves by *C. vellerosus* was also confirmed despite their toxicity (see Kay and Davies 1994).

Feeding generally ranks after resting in the activity budget of colobines, unlike other primates where feeding is the primary activity (for example, *Cercopithecus ascanius*: Cords 1987; *Lagothrix lagothricha*: Defler 1996). The diet

of the *C. vellerosus* group was dominated by leaves, as has been reported elsewhere for this species. However, when compared to other sites, leaves are much less dominant (i.e., 53% vs. 74% in Ghana, Saj *et al.* 2005; Tan 2006; Wong *et al.* 2006). Foods such as fruits, seeds and ants also seem to be important components. This could result either from a locally higher diversity of food resources or a shortage in the preferred food (i.e., leaves); leading to exploration and inclusion of alternative foods in the diet.

Sleeping sites and their characteristics

The monkeys of the Kikélé Sacred Forest chose the Patch 1 forest for their sleeping sites and never slept in Patch 2, the gallery forest. This may be an anti-predation strategy because gallery forest used to be exploited by people from the surrounding villages (i.e., Manigri, Bassila), and colobus monkeys were hunted there over many years. Although there is currently no hunting in the Kikélé Sacred Forest, this finding

Table 2. Food plants consumed by Colobus vellerosus in the Kikélé Sacred Forest, Benin.

Scientific name	Common name (Nagot)	Family	Food item ¹
Afzelia africana	Akpaka	Leguminosae - Caesalpinioideae	UFr
Albizia zygia	Itikpalala	Leguminosae-Mimosoideae	L, UFr, B, Ba
Anarcadium occidentale	Amê gnibo	Anacardiaceae	Fl
Anogeissus leiocarpa	Koloo	Combretaceae	ML
Azadirachta indica	Lili	Meliaceae	YL, ML, Re, St
Cassia sp.	Agbélékokpayan	Leguminosae - Caesalpinioideae	YL
Caesalpinia pulcherrima		Leguminosae - Caesalpinioideae	UFr, F
Ceiba pentandra	Araba	Malvaceae-Bombacoideae	YL
Celtis integrifolia	Afoufè	Ulmaceae	YL, MF, UFr
Cola cordifolia	Kpoé	Sterculiaceae	UFr, Lai,P,B
Cynometra vogelii		Leguminosae-Caesalpinioideae	MF, UFr, S
Daniellia oliveri	Iya	Leguminosae-Caesalpinioideae	UFr
Diospyros mespiliformis	Don'ko	Ebeneceae	Fr
Erythrophleum suaveolens	Ayinyin	Leguminosae - Caesalpinioideae	Fr, UFr
Ficus capensis	Adan Abo	Moraceae	UFr, YL
Ficus congensis	Kpolidi	Moraceae	UFr, YL
Ficus exasperata	Oupi	Moraceae	UFr, YL
Ficus ingens		Moraceae	UFr, YL
Ficus platiphylla		Moraceae	UFr, YL
Ficus polita		Moraceae	UFr
Ficus sycomorus		Moraceae	UFr
Ficus thonningii	Okpoto	Moraceae	YL
Holoptelea grandis	Kpakokpako	Ulmaceae	YL, UFr, B
Khaya senegalensis	Agao	Meliaceae	YL, UFr
Lonchocarpus cyanensens	Elou	Leguminosae - Papilionoideae	Fr
Luffa aethiopica		Curcubitaceae	UFr, L
Mimusops multinervis		Sapotaceae	Fr
Sarcocephalus latifolius	Ewé oïkikoro	Rubiaceae	L
Newbouldia leavis		Bignoniaceae	L
Parinari curratelifolia	Imèdou	Chrysobalanaceae	L
Parkia biglobosa	Igba	Leguminosae - Mimosoideae	Fl
Parquetima nigrescens		Asclepiadaceae	L
Pterocarpus erinaceus	Akpékpé	Leguminosae - Papilionoideae	YL
Strophantus sarmentosus		Apocynaceae	UFr, S, L
Tapinanthus voltensis	Afoman	Loranthaceae	UFr, L

Legend: YL= young leaves; ML= matures leaves; L= leaves; UFr = Unripe fruit; R= resin; Fl= flowers; B= buds; S=seeds; Ba= bark; St= Stem; P= petiole.

Table 3. Comparison of the activity budget of the white-thighed colobus, Colobus vellerosus, at Kikélé with those of other Colobus species.

Species	Group size	Rest	Feed	Move %	Social %	Source
Colobus vellerosus						
Fragments surrounding Boabeng-Fiema	31–33	60	24	12	4	Teichroeb et al. (2003)
	15–16	58	23	17	2	
	7–8	59	24	15	2	
Fragments surrounding Boabeng-Fiema	8, 16, 17	68	22	7	3	Wong and Sicotte (2007)
Kikélé, Benin	13–18	56.64	26.31	13.04	3.13	This study
Colobus polykomos						
Tiwaï, Sierra Leone	9–11	55	31	12	2	Dasilva (1992)
Parc National de Taï, Ivory Coast	14	58	25	16	1	Bitty (unpubl. data)
	11–12	54	21	25	0	
	16	70	11	15	4	
Colobus guereza						
Kibalé, Uganda	9	57	20	5	11	Oates (1977)
Ituri, RDC	8-10	44	26	24	5	Bocian (1997)
Kakamega, Kenya	10–13	63	28	2	6	Fashing (2001)
Colobus angolensis ruwenzorii						
Ituri (RDC)	19–20	52	19	22	5	Bocian (1997)
Nyungwe, Rwanda	>300	32	42	20	5	Fashing et al. (2007)
Colobus angolensis palliatus						
Mbuyu Tundu, Kenya	5–6	64	22	3	4	Wijtten et al. (2012)
Colobus satanas						
Douala-Edea, Cameroun	13–17	54	23	4	13	McKey and Waterman (1982)

may support the hypothesis of predator avoidance in the selection of sleeping sites, as indicated in studies of other primates (for example, *Saguinus mystax* and *S. fuscicollis*: Heymann 1995; *Macaca leonina*: Albert *et al.* 2011) and for *C. vellerosus* by Teichroeb *et al.* (2012). Although there is no predation, in Patch 1 the colobus monkeys chose sleeping trees to rest. Predator avoidance behaviors could also be associated with hunting in the vicinity of the study area, as mentioned above. However, other factors such as reducing time and energy needed for foraging could also determine sleeping tree selection (Anderson 1998).

The physical characteristics of the sleeping sites also support the idea that C. vellerosus at Kikélé selects sleeping sites to avoid predators. The sleeping trees were generally the largest and tallest trees, undoubtedly reducing the chances of predators climbing them. Some large and tall trees, however, were not used as sleeping sites. This was the case for a Ficus sp., Albizia zygia, and Blighia sapida (Sapindaceae); the first two being food species for the colobus monkeys. Selection of sleeping trees is probably also linked to other physical characteristics of the trees. Celtis integrifolia was the species the monkeys slept in most. Compared to the other trees, Celtis integrifolia has very rigid stems and its branches are well spread, which allows for a better distribution of colobus monkeys through the crown and, it could well be more comfortable. However, the monkeys seemed to prefer certain individual trees of the same species despite their similar physical characteristics. This may be a question of habit, or may be linked to their position, which may, for example,

allow for better views of their surroundings (Bovy 2010; Maslarov 2012).

Use of the same sleeping tree on consecutive nights may be due to the lack of predators. In high-risk environments, primates often avoid consecutive use of the same sleeping sites so as to reduce detection by predators (Li *et al.* 2006; Phoonjampa *et al.* 2010). The selection of sleeping trees appears to be a compromise between several factors—species, diameter and height, and location—and the preference of *C. vellerosus* for *C. integrifolia* in Kikélé may also be explained by the fact that it is also used for feeding and resting during the day, with monkeys spending up to eight hours a day on its branches.

Conservation

The white-thighed colobus formerly occurred over a relatively wide swath of West Africa, east of Côte d'Ivoire from between the Sassandra and Bandama rivers to western Nigeria. It occurs in a number of protected areas, but hunting (primarily) and habitat loss are now major threats. It is declining fast in Côte d'Ivoire, rare in Benin and Togo, possibly extinct in Nigeria, and heavily hunted in Ghana (Gonedelé Bi *et al.* 2010; Oates 2011). Ginn and Nekaris (2014) indicated that it may have been extirpated already from southern Burkina Faso. Its survival will be strongly dependent on small sanctuaries and forest reserves, such as those in Benin. The permanence of the single troop in the Kikélé Sacred Forest and the other small populations in forest patches and forest reserves

will depend on careful management, which will demand a good understanding of their population dynamics and ecological needs with regard to food resources and sleeping sites. Our study suggests that *C. vellerosus* shows an activity pattern similar to most colobines elsewhere. However, its diet seemed to be more balanced between leaves and other items such as fruits, seeds, ants, buds, bark, flowers, gum, and inflorescences. The choice of sleeping trees indicates persistence of predation avoidance behaviors despite the absence of predators. As Oates (2011) pointed out, hunting for its meat and fur is the main threat, exacerbated by logging and forest destruction since the 1970s. As such, translocation, forest restoration and active meta-population management are predictably the necessary future steps for its conservation.

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Distribution and Conservation Status of the Mount Kilimanjaro Guereza *Colobus guereza caudatus* Thomas, 1885

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Abstract: The Mount Kilimanjaro guereza *Colobus guereza caudatus* is considered to be endemic to northeast Tanzania. This paper presents the first records for *C. g. caudatus* in Kenya, describes the distribution of this subspecies, and assesses its conservation status. In September 2014, we found *C. g. caudatus* in southeast Kenya in Kitobo Forest Reserve (1.6 km²) and Loitokitok Forest Reserve (4.2 km²). This subspecies has an altitudinal range of *c.* 660–3,050 m asl and an 'Extent of Occurrence' of *c.* 4,040 km². These findings are important as they: (1) add one subspecies of primate to Kenya's primate list; (2) remove one endemic subspecies of primate from Tanzania's primate list; (3) establish *C. g. caudatus* as the most threatened primate subspecies in Kenya; (4) change the priorities for actions necessary to maintain Kenya's primate diversity; and (5) indicate that detailed biodiversity surveys within Kitobo Forest and Loitokitok Forest are likely to yield new data crucial to the conservation of biodiversity in southeast Kenya.

Key Words: biogeography, *Colobus guereza caudatus*, colobus monkey, Kenya, Kitobo Forest, Loitokitok Forest, Mount Kilimanjaro

Introduction

Africa harbors a high diversity of primates, most of which are endemic to the continent. Of the 25 genera and 93 species of primate in Africa, 12 genera, 19 species, and 24 subspecies occur in Kenya (De Jong and Butynski 2012). Although primates are one of the best studied taxonomic groups in East Africa, many questions remain concerning their taxonomy, biogeography, abundance, and conservation status.

The large (c. 10 kg), arboreal, guereza colobus *Colobus guereza* Rüppell, 1835, is endemic to Africa. Eight subspecies are currently recognized (Napier 1985; Groves 2001, 2007; Grubb *et al.* 2003; Fashing and Oates 2013; Groves and Ting 2013), three of which occur in Kenya; Mau Forest guereza *C. g. matschiei* Neumann, 1899 (Fig. 1), Mount Kenya guereza *C. g. kikuyuensis* Lönnberg, 1912 (Fig. 2), and Mount Uarges guereza *C. g. percivali* Heller, 1913. The latter two subspecies are endemic to central Kenya.

The Mount Kilimanjaro guereza *C. g. caudatus* is considered to be endemic to northeast Tanzania (Fig. 3), occurring on Mount Kilimanjaro and Mount Meru (Matschie 1895; Kingdon 1971; Rodgers 1981; Groves 2001, 2007; Fashing and Oates 2013), with smaller populations in several forest

reserves on the lower south and east slopes of Mount Kilimanjaro (Napier 1985; Grimshaw *et al.* 1995; Foley *et al.* 2014). These include Rau, Kahe I, Kahe II, and Kileo Forest Reserves (Fig. 4). *Colobus guereza* is well known for its ability to persist, sometimes at high density, in small, isolated, disturbed, forest patches (Fashing and Oates 2013).

This paper is primarily concerned with presenting the first records for *C. g. caudatus* in Kenya, and with the distribution and conservation status of this subspecies.

Methods

Diagnostic phenotypic traits for the subspecies of *C. guereza* are presented in Dandelot (1974), Napier (1985), Groves (2001, 2007), and Fashing and Oates (2014). Drawings on Plate 45 in Mittermeier *et al.* (2013, p.698) provide a visual comparison of the eight subspecies of *C. guereza*. In the field, the primary diagnostic traits for *C. g. caudatus* are as follows: white mantle hairs cover >29% of the base of the tail, proximal part of the tail is black with scattered grey hairs, 71–88% of the tail is white, and the white tail tuft is very full (Figs. 3, 5 and 6).



Figure 1. Adult male Mau Forest guereza *Colobus guereza matschiei*, Lake Naivasha, southwest Kenya. In this subspecies, 36–57% of the tail is white. Photograph by Yvonne A. de Jong and Thomas M. Butynski.

Primate surveys were conducted 27–28 September 2014 from a vehicle and on foot by the two authors. Transects were run along dirt roads and foot paths. These were selected to maximize the chances of encountering as many individuals of as many species of primate as possible. As time was very limited, the rapid assessment survey method was used, as described in Butynski and Koster (1994), White and Edwards (2000), and Butynski and De Jong (2012).

Zeiss Victory 10×42 and Zeiss Dialyt 7×42B binoculars were used to scan for primates. Photographs were taken with a Nikon D200 digital camera fitted with a Nikon 80–400 mm lens, and with a Canon EOS 40D digital camera fitted with a Canon 100–400 mm lens. Photographs were shot in 'raw' format. As many individuals as possible in each primate group were photographed. All primate encounters were mapped with the help of a GPS (Garmin Oregon 650), Garmin MapSource v. 6.14 software (Garmin, Olathe, USA), and MapInfo Professional v. 10.5 software (Pitney Bowes Mapinfo, Troy, USA).

Literature and museum databases (for example, GBIF 2015) were searched to obtain locality records for *C. g.*



Figure 2. Adult male Mount Kenya guereza *Colobus guereza kikuyuensis*, Nanyuki, central Kenya. In this subspecies, 71–81% of the tail is white. Photograph by Yvonne A. de Jong and Thomas M. Butynski.

caudatus. Additional locality records were obtained from our own field notes, through correspondence with colleagues, and through iNaturalist (De Jong and Butynski 2015). These records were used to map the geographic range and estimate the 'Extent of Occurrence' (IUCN 2001).

Kitobo Forest Reserve

Kenya's Kitobo Forest Reserve (03.44375°S, 37.62165°E) is a coastal forest located in Taita-Taveta County. This small (1.6 km²), indigenous, evergreen, closed-canopy forest lies at c. 750 m asl on the lower southeast slope of Mount Kilimanjaro (c. 2 km east of the Tanzania border, c. 10 km south-southwest of Taveta, and c. 225 km northwest of the Indian Ocean; Fig. 4). Kitobo is a groundwater forest supported by springs that originate on Mount Kilimanjaro, particularly the Njoro Spring. This forest is isolated, lying in a vast semi-arid region of grassland, woodland, and bushland dominated by species of acacia *Acacia* (Fabaceae) and commiphora *Commiphora*

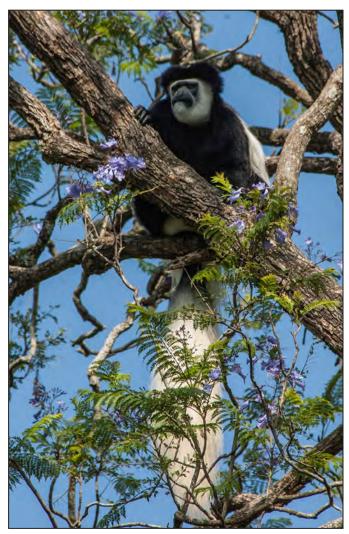


Figure 3. Adult male Mount Kilimanjaro guereza *Colobus guereza caudatus*, Usa River, northeast Tanzania. In this subspecies, 71–88% of the tail is white and the tail tuft is extremely full. Photograph by Yvonne A. de Jong and Thomas M. Butynski.

(Burseraceae). Mean annual rainfall is *c*. 600 mm and mean annual temperature is *c*. 23°C (<climate-data.org>).

Kitobo is surrounded by small-holder farms on which the main crops are maize, rice, beans, bananas, and mangoes. The more common emergent trees in Kitobo include *Acacia xanthophloea, Albizia glaberrima* (Mimosaceae), *Celtis africana* (Ulmaceae), *Cordyla africana* (Caesalpiniaceae), *Diospyros mespiliformis* (Ebenaceae), *Ficus* spp. (Moraceae), *Milicia excelsa* (Moraceae), *Newtonia buchananii* (Mimosaceae), and *Trichilia emetica* (Meliaceae) (NEMA 2009). Kitobo is one of the most important sites in Kenya for the conservation of reptiles and amphibians (Malonza *et. al.* 2011), and supports at least three threatened bird species (Mlamba *et al.* 2013).

The authors conducted a survey of the primates of Kitobo from 14:00 h on 27 September until 08:00 h on 28 September 2014. Three groups of *C. g. caudatus* (composed of at least 6, 6, and 8 individuals) were encountered (Fig. 5; also Butynski and De Jong 2015). Based on the choruses of loud 'roar' calls heard during the night and early morning, there are at least six

groups of *C. g. caudatus* in Kitobo. This is the first record for *C. g. caudatus* in Kenya. Kitobo, at 750 m asl, is considerably lower than the next lowest site in Kenya for *C. guereza* (*C. g. kikuyuensis* is present at *c.* 1,720 m asl near Nairobi).

Five other primates are found in Kitobo. We encountered at least eight groups of Zanzibar Sykes's monkeys *Cercopithecus mitis albogularis*, one group of central yellow baboons *Papio cynocephalus cynocephalus*, one group of Hilgert's vervet monkeys *Chlorocebus pygerythrus hilgerti*, 10–15 Pangani small-eared galagos *Otolemur garnettii panganiensis*, and four Kenya lesser galagos *Galago senegalensis braccatus*. With six species, the primate community of Kitobo is surprisingly diverse considering its small size, isolation, and semi-arid surroundings. Overall primate abundance is high.

Loitokitok Forest Reserve

Little remains of the indigenous montane forest that once occurred in Kenya's Kajiado District on the lower north slope of Mount Kilimanjaro. In 2000, only c. 4.2 km² of the area was covered with forest, representing a 35% decline in forest cover since 1973 (Campbell et al. 2003). The forest fragments that remain are located south (up-hill) from the town of Loitokitok (= Oloitokitok) in the Loitokitok Forest Reserve on the Kenya-Tanzania border (Fig. 4). Loitokitok is c. 57 km north-northwest of Kitobo. Mean annual rainfall is c. 900 mm and mean annual temperature is c. 18°C (<climate-data.org>). The more common tree species here include Acacia spp., pencil cedar Juniperus procera (Cupressaceae), wild olive Olea europaea (Oleaceae), cabbage tree Cussonia holstii (Araliaceae), croton Croton megalocarpus (Euphorbiaceae), Ficus spp., and several exotics, particularly eucalyptus Eucalyptus (Myrtaceae).

On 28 September 2014, during 13:00–15:30 h, we conducted a primate survey in forest on the property of the Outward Bound Trust at Loitokitok. One group of *C. g. caudatus*, composed of two adult males, was encountered *c.* 800 m into Kenya from the Tanzania border (02.94368°S; 37.50682°E; 1,835 m asl; Fig. 6). It is likely that additional groups were present. According to the staff of the Outward Bound Trust, the only other diurnal primate here is *C. m. albogularis*.

Distribution and Conservation Status of *Colobus guereza* caudatus

Colobus g. caudatus was first discribed and named by Oldfield Thomas (1885) based on a specimen collected by Harry Johnston in 1883 at Useri, Tanzania, on the northeast slope of Mount Kilimanjaro (03.08098°S; 37.59384°E; 915 m asl). Useri is c. 8 km southwest of the Kenya border, c. 40 km north of Kitobo, and c. 20 km south-southeast of Loitokitok (Fig. 4). Kitobo is probably the eastern limit for C. g. caudatus and Loitokitok is probably the northern limit.

There are some errors in the literature and on the internet as concerns claimed localities for *C. g. caudatus* (which include localities in Burundi and Ethiopia). Some of this is

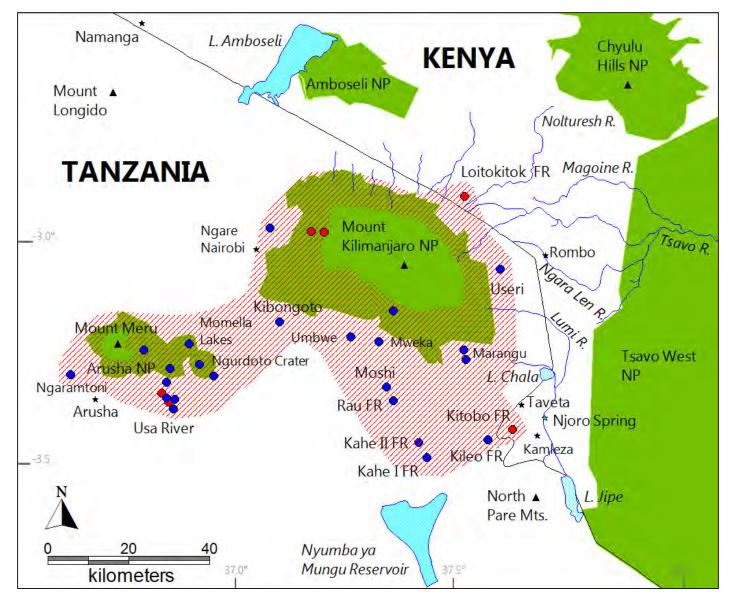


Figure 4. Distribution of the Mount Kilimanjaro guereza *Colobus guereza caudatus*. 'Extent of Occurrence' is depicted by the red polygon (*c.* 4,040 km²). Areas of Mount Kilimanjaro and Mount Meru >3,050 m asl are excluded from the polygon as *C. g. caudatus* is not known to occur above this altitude. Green represents national parks. Red dots represent sites where T. M. Butynski and Y. A. de Jong encountered *C. g. caudatus*. Blue dots represent other sites for *C. g. caudatus* (Thomas 1885; Lönnberg 1910; Schwarz 1929; Rodgers 1981; Napier 1985; Grimshaw *et al.* 1995; Foley *et al.* 2014; De Jong and Butynski 2015; GBIF 2015; N. J. Cordeiro pers. comm.; A. Semerdjian pers. comm.; M. Grimm pers. comm.; J. A. Ratzlaff pers. comm.; R. Knocker pers. comm.; F. Reid pers. comm.). Only the rivers draining Mount Kilimanjaro into Kenya are shown.

due to misidentified museum specimens, and also, perhaps, to the application of a taxonomy in use at the time. For example, *C. guereza* specimen ZS.1935.3.14.1 at the Natural History Museum (London) is referred to *C. g. caudatus* by Napier (1985). This specimen was obtained at Handajega in the western Serengeti. As such, it should be referred to *C. g. matschiei*. The Global Biodiversity Information Facility database (GBIF 2015) presents additional examples of this problem. For the purposes of establishing the distribution of *C. g. caudatus*, we accepted no records for west of the Eastern (Gregory) Rift Valley (i.e., west of 36°E), west and northwest of which *C. g. matschie* occurs, or for north of the lower north slope of Mount Kilimanjaro (i.e., <1,800 m asl, north of 02.8°S), north of which *C. g. kikuyuensis* occurs (Kingdon 1971; Napier 1985; Fashing and Oates 2013; Y. A.

de Jong and T. M. Butynski pers. obs.). Locality records for *C. g. caudatus* beyond these western and northern limits are considered to be erroneous (Fig. 4).

Colobus g. caudatus is the southeastern-most subspecies of C. guereza and is isolated from other subspecies by large expanses of unsuitable (semi-arid) habitats. The nearest known population of C. g. kikuyuensis is c. 170 km to the north-northwest in the Ngong Hills (Napier 1985), while the nearest known population of C. g. matschie is c. 160 km to the northwest in the Loita Hills (Butynski and De Jong 2012). The nearest known population of another species of colobine is that of Peters's Angola colobus Colobus angolensis palliatus, c. 75 km to the southeast in the South Pare Mountains (Rodgers 1981). Contrary to what is stated in Foley et al. (2014), C. guereza is not present in the North Pare Mountains



Figure 5. Adult male Mount Kilimanjaro guereza *Colobus guereza caudatus*, Kitobo Forest Reserve, southeast Kenya. Photograph by Yvonne A. de Jong and Thomas M. Butynski.

(Rodgers 1981; Cordeiro *et al.* 2005; Doggart *et al.* 2008; T. M. Butynski and Y. A. de Jong pers. obs.). The absence of *C. guereza* and *C. angolensis* from the North Pare Mountains is unexpected given the proximity of these mountains to populations of these two species; *C. guereza* at Kileo and Kitobo *c.* 15 km to the northwest, and *C. angolensis* in the South Pare Mountains *c.* 7 km to the southeast.

Almost all of Mount Kilimanjaro lies in Tanzania; the lower slopes to the north and east extend into extreme south Kenya. Despite the proximity of Kitobo and Loitokito to known sites for *C. g. caudatus* in Tanzania, there are no written records or specimens of *C. g. caudatus* for Kenya. As such, this subspecies has always been considered an endemic to Tanzania. De Jong and Butynski (2012) list *C. g. caudatus* as endemic to Tanzania but indicated that this subspecies might be present in extreme south Kenya. The nearest record of *C. g. caudatus* to Kitobo is from Kileo Forest Reserve in Tanzania (03.46054°S; 37.57005°E; 730 m asl; Doggart *et al.* 2008). Kileo (*c.* 1 km²) lies *c.* 1.9 km southwest of the Kenya border and *c.* 6 km southwest of Kitobo (Fig. 4).

Colobus g. caudatus is widespread on Mount Kilimanjaro and Mount Meru, being present at many more localities on these two mountains than indicated in Figure 4. In Tanzania, this subspecies occurs as low as 660 m asl in Kahe II Forest Reserve (Cordeiro et al. 1995; N. J. Cordeiro pers. comm.)



Figure 6. Adult male Mount Kilimanjaro guereza *Colobus guereza caudatus*, Loitokitok, southeast Kenya. Photograph by Yvonne A. de Jong and Thomas M. Butynski. For additional images and localities for *C. guereza*, visit the 'Colobinae Photographic Map' at <www.wildsolutions.nl>.

and as high as at least 3,050 m asl on Mount Kilimanjaro (Guest and Leedal 1954). Grimshaw *et al.* (1995) and Foley *et al.* (2014) report that on Mount Kilimanjaro *C. g. caudatus* is most common on the north and west slopes between 1,800 m and 2,300 m asl.

The overall current Extent of Occurrence of C. g. caudatus is c. 4,040 km² (Fig. 4). In Kenya, the Extent of Occurrence is <80 km², or <2% of the overall Extent of Occurrence. The 'Area of Occupancy'(IUCN 2001) in Kenya is probably <6 km². The number of C. g. caudatus in Tanzania is likely well over 10,000, whereas in Kenya the number is unlikely to be >200. The population of C. g. caudatus in both countries must be in decline in response to on-going habitat degradation, loss and fragmentation.

The IUCN Degree of Threat Category for *C. g. caudatus* has never been assessed (IUCN 2015). Applying the current *IUCN Red List Categories and Criteria* (IUCN 2001), a taxon with a declining, fragmented, population, and an Extent of Occurrence of <5,000 km², is 'Endangered', whereas a taxon with a declining, fragmented, population, and an Extent of Occurrence of <100 km², is 'Critically Endangered'. Therefore, once assessed by IUCN, *C. g. caudatus* is expected to be listed as an 'Endangered' subspecies. In Kenya, *C. g. caudatus* is expected to be listed as a nationally 'Critically Endangered' subspecies.

Primate Conservation in Taita-Taveta County and Kajiado County

Kitobo and Loitokitok are likely the only two sites in Kenya where *C. g. caudatus* occurs. Nonetheless, additional, more comprehensive, primate surveys should be undertaken in the forests of Taita-Taveta County and Kajiado County, with a focus on locating more populations of *C. g. caudatus*. For each forest, the survey should assess which species of primate are present, and their abundance, conservation status, and threats. These surveys should focus on ground water forests (for example, Rombo and Kamleza), as well as forest along the rivers that flow from Mount Kilimanjaro into Kenya, including the Rombo (or Ngara Len), Lumi, and Nolturesh, and the many seasonal streams along the Kenya-Tanzania border.

Although *C. g. caudatus* is reasonably well protected in the forest reserves and national parks where it occurs in Tanzania (Rodgers 1981; Foley *et al.* 2014), it is under severe threat in Kenya. The human population in Taita-Taveta County and Kajiado County has increased about five-fold in just the past 30 years. One result is that indigenous forest now covers <0.02% of the landscape (Campbell *et al.* 2003; NEMA 2009). Current pressure to unsustainably exploit the few remaining forests is extremely high. Most, if not all, forests in these two counties suffer from degradation, loss, and fragmentation, and all are small.

Given the circumstances as concerns forest and biodiversity conservation, Taita-Taveta County and Kajiado County, the Kenya Wildlife Service, Kenya Forest Service, county authorities, and people living around Kitobo Forest and Loitokitok Forest, should give particular attention to the long-term survival of these two small forests as their loss will probably mean the extirpation of several vertebrate species from both counties, and of *C. g. caudatus* from Kenya.

Conclusions

The findings presented here are important as they: (1) add one subspecies of primate to Kenya's primate list (now 25 subspecies); (2) remove one endemic subspecies of primate from Tanzania's primate list; (3) establish *C. g. caudatus* as the most threatened primate subspecies in Kenya; (4) change the priorities for actions required to maintain Kenya's primate diversity; and (5) indicate that detailed biodiversity surveys within Kitobo Forest (particularly) and Loitokitok Forest are likely to yield new data crucial to the conservation of biodiversity in southeast Kenya.

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Geza Teleki and the Emergence of Sierra Leone's Wildlife Conservation Movement

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Abstract: This paper details Geza Teleki's contributions in the development of a wildlife conservation movement in Sierra Leone in the late 1970s to early 1980s. Teleki, a primatologist researcher and an animal rights activist, arrived in Sierra Leone in 1979 to find an inactive government wildlife conservation program and a thriving primate export sector. Shocked by what he saw, he worked with local and international environmentalists to build a wildlife conservationist movement in Sierra Leone. From capricious negotiations with presidential dictator Siaka Stevens to theurgical conflicts with local communities, Teleki helped to lay the groundwork for transforming wildlife conservation in the small West African nation. In this paper, I explore these contributions, reconstructing Teleki's position as a historical actor in Sierra Leone as well as providing some reflection on how the legacy of his work has been inscribed upon Sierra Leone's contemporary wildlife conservation landscape.

Key Words: Africa, history, Geza Teleki, Outamba-Kilimi National Park, Sierra Leone, wildlife conservation

Introduction

After a long and distinguished career of primatological research, environmental conservation and animal rights activism, Dr Geza Teleki passed away on 7 January 2014. One of his more notable accomplishments came from his work in the West African country of Sierra Leone in the late 1970s to early 1980s. During this period, he helped to form a nascent Sierra Leonean wildlife conservation movement, and subsequently became a central figure in eliminating the country's chimpanzee export trade as well as being a driving force behind the establishment of its first national park. This work included Teleki negotiating directly with the country's president, a (sometimes conflictive) working relationship with forest-edge village communities, as well as countering individuals in the wildlife export trade. Despite this prominent role, however, and although a number of histories of wildlife conservation have been written on Sierra Leone (for example, Jones 1998; Oates 1999), there has been surprisingly little analysis of Teleki's time there and how the broader legacy of his work has been inscribed upon Sierra Leone's contemporary wildlife conservation landscape and movement. In this paper, I address this gap, reconstructing Teleki's position as

a historical actor in Sierra Leone as well as providing some reflections on his broader influence.

To do this, I draw data from a number of interviews with wildlife conservation actors in Sierra Leone, including one with Geza Teleki in 2012, and with a number of staff of Sierra Leone's Outamba-Kilimi National Park, who worked with Teleki in the 1980s. I also draw upon archival data which was collected from Sierra Leone (i.e., Fourah Bay College Library, Sierra Leone National Archives, Njala University College Library, the Outamba-Kilimi Office) and the United Kingdom (British Library, the UK National Archives, and the Harrison Institute), as well from private collections and online sites. I also made field visits to relevant conservation sites across Sierra Leone, including the Outamba-Kilmi National Park, where Teleki was based for much of his time in Sierra Leone. This data was collected in 2011 and 2012.

The remainder of this article is divided into three sections. The first provides a history of wildlife conservation in Sierra Leone prior to Teleki's arrival, contextualizing the political economy and challenges that Teleki encountered upon arriving in the late 1970s. The subsequent section provides a history of Teleki's time in Sierra Leone, detailing his efforts in curtailing wildlife exports and establishing Outamba-Kilimi

National Park. The final section of the article provides some reflection on Teleki's legacy in Sierra Leone.

Early Wildlife Conservation in Sierra Leone

Although wildlife conservation legislation had been passed as early as 1901 in Sierra Leone, the British Colonial government that administered Sierra Leone until 1961 made only limited efforts to enact wildlife conservation programs across the country (Jones 1998; Munro 2015). Early on, the colonial government largely considered it to be a peripheral issue and tended to assume there were no major threats that would cause a significant decline in wildlife population numbers (Granville 1931; Stanley 1933a, 1933b; Stocks 1931). This situation changed marginally towards the end of the colonial period, and a Committee for the Preservation of Flora and Fauna was set up in 1960 (Hill, 1963). Subsequently, after the country's independence, the work of this committee translated in 1967 into the establishment of a Wildlife Branch under the Forestry Department and the passing of the Wildlife Conservation Act in 1972 (Lowes 1970; Jones 1988).

Despite these administrative and legislative achievements, there was limited enthusiasm within the Government for wildlife conservation initiatives during this period (Tuboku-Metzger 1979; Jones 1998). Sierra Leone at the time was being run by the authoritarian government of President Siaka Stevens (the country's effective head of state from 1967 until 1985), who governed through a system of acute patrimonialism, whereby key influential individuals were appeased with strategic favors and payments (Bøås 2001; Richards 1996). In this context, a 'shadow state' emerged, revolving predominantly around Sierra Leone's rich mineral resource extraction, with only a small elite minority ever profiting substantially from it (Reno 1995).

The implications of this for conservation were that forests were largely viewed as sources of timber and revenue, and as such the establishment of controversial large-scale logging concessions was common (Tuboku-Metzger 1983; Munro and Hiemstra-van der Horst 2011; Hiemstra-van der Horst et al. 2011). Concomitantly, the Forestry Department had more of an interest in wildlife's commercial potential, rather than its overall protection. Joshua Sawyerr (the head of the Department from 1963 to 1975), openly supported foreign hunters coming to Sierra Leone: "We aren't bothered by the hunter from abroad, who does it for sport. He shoots one elephant, for which he will pay in hard currency and then go away. It's [sic] our own people who are the danger" (Sawyerr cited in: FAO Release, 1971); while Musa Feika (Sawyerr's successor, who headed the Department until 1983) personally signed off and approved wildlife export shipments, even after the activity was officially banned (Anonymous 1983b, 1986; Peterson and Goodall 1993). As Grainger and Konteh (2007, p.54) noted, during the Siaka Stevens' era, Forestry Department operations became highly concentrated in the Head of the Forestry Department (i.e., Sawyerr and Feika), a figure tied by personalized neopatrimonial connections to the president, which ensured "that the Forestry [Department] literally spoke with a 'single voice' in policy formulation." Thus, Sawyerr and Feika were very much able set the tone for formal government wildlife conservation policy during the 1960s and 1970s.

This governmental emphasis on wildlife as a commercial commodity was perhaps unsurprising as the exportation and trade of animals, and chimpanzees in particular, had emerged as a lucrative enterprise in Sierra Leone. As early as the 1920s, Henry Trefflich, a famed animal dealer from New York, set up an animal export outpost in Freetown, where he then proceeded to export hundreds of chimpanzees, among other animals. One of Trefflich's biggest customers was NASA, with many Sierra Leonean chimpanzees reportedly being used in the Agency's flight testing programs (Trefflich and Anthony 1967). Building upon this early trade, during the 1950s two men emerged as the main agents of Sierra Leone's animal export trade: Suleiman Mansaray and Franz Sitter. Mansaray, a Sierra Leonean national, appears to have taken over Trefflich's old animal export business, while Sitter, originally an Austrian national, arrived in Sierra Leone sometime during the 1950s (Teleki 1980a). Sitter's history prior to his arrival has been the center of much debate, with a number of people alleging that he was a former Nazi who fled to Sierra Leone after the fall of the Third Reich (Peterson and Goodall 1993; McGreal 2014). Although this claim could never be fully substantiated, Sitter's unknown, potentially dubious, past helped in typecasting him as a prominent villain in the eyes of the wildlife conservation movement (see Peterson and Goodall 1993; McGreal 2014).

Mansaray specialized in birds, while Sitter specialized in reptiles, but both men dealt in primate exports which proved to be the most lucrative trade of all (Anonymous 1961; Teleki and Baldwin 1981). Teleki (1986), drawing upon government records, estimated that between them, Mansaray and Sitter exported around 2,000 chimpanzees during the 1970s alone (see also Teleki and Baldwin 1981). Most of them were destined for medical testing laboratories in the United States, meaning that the vast majority of chimpanzees used in medical testing during this period would have originated from Sierra Leone (Anonymous 1978; Peterson and Goodall 1993; Sawyerr 1963; Teleki 1986).

This vast trade, however, did not occur without opposition, and in 1976 Freetown resident Daphne Tuboku-Metzger, who had an interest in wildlife conservation since her school years (Tuboku-Metzger 1999), established Sierra Leone's first environmental NGO – the Sierra Leone Environment and Nature Conservation Association (SLENCA) (Anonymous 1977; Polunin and Curme 1997). The organization quickly succeeded in gaining a profile in the local and international media, and focused on curtailing the country's wildlife exports and setting up wildlife sanctuaries (Anonymous 1978; Tuboku-Metzger 1979, 1991). SLENCA had some early success in lobbying Siaka Stevens, with the President establishing a moratorium on chimpanzee exports in 1978. The declaration of the moratorium, however, proved to be largely symbolic, and within months of the export ban, eight



Figure 1. Sierra Leonean chimpanzees seized at Amsterdam Airport in 1979 (Anonymous 1979).

chimpanzees shipped from Sierra Leone were confiscated at Schipol Airport in Amsterdam because of a lack of import permits (see Fig. 1). The chimpanzees had been shipped by Franz Sitter, and the incident ultimately helped to focus international attention on Sierra Leone's trade in wildlife exports, indirectly resulting in the commissioning of Teleki's first visit to Sierra Leone (Anonymous 1979; Teleki 1986).

Geza Teleki Arrives

Amid these growing international concerns surrounding the live animal trade, in 1979 Geza Teleki was asked by the United States' Government to provide advice on the trade of chimpanzees being imported into medical laboratories. Teleki had a background in primate protection activities. He sat on the board of the International Primate Protection League (IPPL), and had previously worked on chimpanzee conservation programs with Jane Goodall in East Africa. After some desk-based research, Teleki was surprised to find that almost all of the chimpanzees being used for medical testing in the US were not only coming from "one small country in West Africa," Sierra Leone, but also from one dealer, Franz Sitter (Teleki 1980a; Teleki pers. comm. 2012). He therefore proceeded to secure funds to finance a fact-finding mission, and travelled to Sierra Leone in late 1979, where he teamed up with Tuboku-Metzger and SLENCA to conduct a survey of the chimpanzee population in the country and to evaluate the impact of the primate export industry (Teleki pers. comm.

2012). The findings were designed to influence Sierra Leone's policy and feed into broader international campaigns for primate protection (Anonymous 1980, 1983).

Teleki's findings painted a dismal picture of wildlife conservation in Sierra Leone. From his surveys of the country's forest reserves he deduced that there were only 2,000 chimpanzees left in the country, and that the operations of Sitter, along with those of Mansaray, had decimated the primate population (Teleki, 1980a): "it was a very dismal experience in those six months. I must have travelled close to 10,000 kilometres around the country, I visited all the forest reserve areas, and found virtually nothing remaining" (Teleki pers. comm. 2012). Teleki took these findings to President Siaka Stevens, and a process of negotiation to improve the conservation of the country's wildlife ensued. Despite Siaka Stevens' notorious reputation as a dictator, Teleki reflected jovially on his conversations with the President:

He was a character. He was an exploiter, but he did it with charm. You knew you were talking to a crook, but at the same time it was an enjoyable conversation. He used analogies all of the time. [I would say] "Don't you think you could shut down some of Sitter's operations because I can't raise money in America if you let all these chimps go." He would respond with something like "well Mr Teleki my bucket has a hole in it, and I need you to help me plug up the hole" ... [thus I requested that he should] do what he could to shut down the export of wildlife from Sierra Leone, and in return he requested that I go back to the United States and raise money to set up the nation's first national park (Teleki pers. comm. 2012).

The negotiations thus reached a discreet compromise, Siaka Stevens would enforce an overall ban on animal exports, if Teleki was able to source overseas funding to make up for the loss in governmental revenue, and to finance the establishment of Sierra Leone's first national park. Critical for these negotiations was Sierra Leone's upcoming hosting of the Organisation of African Unity (OAU) conference in 1981/1982 (Kandeh 1999). Prior to the OAU conference, Stevens' government had been criticized both internationally and regionally for its human rights abuses, its undemocratic reforms, and overall poor governance. Stevens needed to construct some 'positive' aspect of his government to present during the conference. Teleki noted the fortunate timing of the event:

His support was purely mercenary ... For the upcoming OAU meeting, he badly needed to promote [his government] in a positive way, because he was constantly getting kicked for illegal diamond exports and other bad things going on in Sierra Leone at the time. So he wanted a flag that he could wave, so he could say, "we are not so bad. We are trying to make

a national park." So it was simply fortunate timing on my part (Teleki pers. comm. 2012).

Teleki continually appealed to Stevens' hubris to gain further support for the national park (Teleki pers. comm. 2012), as his letters to the President reveal:

Perhaps the suggestion that Your Excellency makes the announcement of an Outamba-Kilimi National Park at the upcoming OAU conference would not be out of order, as I am sure that such a statement would be applauded by many world leaders (Teleki 1980c).

I therefore urge Your Excellency to extend a total ban to exports of *all* wildlife until an adequate number of Game Reserves and National Parks have been established and developed with financial aid and expert advice from overseas organizations ... I respectfully submit that Your Excellency considers a formal statement to this effect being made at the upcoming OAU conference in Freetown, as I am sure such a step would bring praise from the leaders of other African nations where wildlife is strictly protected, and also from overseas governments and conservation organizations backing wildlife protection throughout Africa (Teleki 1980b).

The national park was to be in the Tambakha Chiefdom in the northeast of Sierra Leone. It was the site that had been identified as promising as early as 1963, but progress in converting it into a national park had, for the previous decade and a half, been limited to a few pronouncements in the Government Gazette and the occasional survey (Teleki and Bangura 1981; McGiffin 1985b; Teleki 1986; Waugh 1986). Politically, it was a safe site for a national park as far as Siaka Stevens was concerned; the area had few people and low soil fertility and therefore limited large-scale agriculture potential (Teleki pers. comm 2012). It was also well outside the country's forestry and mining operations, and would not as such compromise government revenue—formal and informal (Teleki pers. comm. 2012). During the 1970s, the site of the proposed park had become the focus of Sitter's animal hunting and operations, while missionaries had also been involved in regular elephant hunting expeditions in the area (Teleki 1980a, 1986; McGiffin 1985a); and therefore, for Teleki, the "conservation of Outamba and Kilimi [was] a matter of life and death" (Anonymous 1980, p.14). Teleki continued to pressure Stevens and, using his international contacts, he obtained support from IUCN and World Wildlife Fund-US. WWF-US played a major role in Teleki's efforts to create the national park, particularly through its President, Russell Train, a Vice President, E. U. Curtis "Buff" Bohlen, and Russell Mittermeier, then Director of the organization's Primate Program. Bohlen was especially important to the project, and was responsible for

allocating a large chunk of funding to it in those early days. Indeed during that period, Outamba-Kilimi was one of WWF-US's largest programs worldwide and the organization was likely the biggest supporter of Teleki's efforts at that time. Teleki subsequently acted as the director of the park between 1981 and 1984, and research on wildlife was initiated in the area during this period (for example, Harding and Harding 1982; Harding 1984; Zug 1987; Happel, 1988; Teleki *et al.* 1990).

Teleki, along with other wildlife conservation activists in Sierra Leone, appeared to have some success in influencing the President. Stevens approved all of the OKNP proposals and in 1982 a ban on all wildlife exports was (re)enacted (McGiffin 1985b). The latter had some effect, and the wildlife exporter Mansaray went out of business around this time. Sitter's operations, however, persevered, albeit on a much more limited scale (Teleki 1986; Teleki pers. comm. 2012). Teleki personally worked on establishing Outamba-Kilimi until 1984; however, he fell short of being able to have the area declared a national park. The main issue delaying its formation was the financing of the resettlement and compensation of several hundred people living within the Park's proposed boundaries (Harding and Harding 1982; Teleki 1986). While Geza recalled that he had a good relationship with most communities around the Park, he detailed that some hostile resistance emerged with one chief and his community that were to be moved as a result of a Park's gazettement: "He [The Chief] spent a great deal of time trying to use black magic on me and only stopped when I started using it on him, and then he became scared enough to not do it anymore" (Teleki pers. comm. 2012). Despite the conflict (and Teleki's somewhat controversial response to it), Teleki ascribed the lack of progress to the central government that did not want to provide any form of compensation (Teleki pers. comm. 2012).

Teleki left Sierra Leone in 1984 due to frustrations with local politics that slowed progress in achieving conservation outcomes, along with deterioration in his health. He reflected that his wildlife conservation efforts would be best utilized at the international level: "When you get into a situation like I did in Sierra Leone, the people who do the nasty stuff always find another market. I found that it was kind of useless to do this at the source end" (Teleki pers. comm. 2012). He thus returned to the United States where he continued to work, campaigning to improve the lives of both wild and captive chimpanzees (Harding 2014).

Geza Teleki's Legacy in Sierra Leone

Teleki thus left Sierra Leone with chimpanzee exports still occurring and with Outamba-Kilimi still not formally declared a national park. His two main wildlife conservation

¹ Teleki's experience of River Blindness (Onchocerciasis) infection, likely contracted during his time in the Outamaba-Kilimi region, was examined in the documentary series "Monsters Inside Me" (2009), produced by Animal Planet.



Figure 2. Geza Teleki at Outamba-Kilimi National Park (OKNP) in 1983 The photo was published in the *Solarex Current* (1985) magazine for an article discussing Teleki's and OKNP's pioneering use of solar power at the main campsite (Anonymous 1985). Photograph provided by Geza Teleki in 2012.

objectives—ending animal exports and establishing a national park—although having progressed, had not been fully realized. Nevertheless, he had helped to provide a critical foundation for future conservation and, after a number of vicis-situdes, both objectives would eventually be realized, thanks to wildlife conservationists that followed and built upon and expanded his work.

Teleki's attempt to eliminate the export of chimpanzees was mainly frustrated by the persistence of Franz Sitter's operations. In 1983, despite the animal export ban, Sitter shipped 50 Sierra Leone chimpanzees to a Japanese pharmaceutical company. It appears that the exports were allowed in exchange for an aid shipment of rice from the Japanese Government (Anonymous 1983b, 1986; Kabasawa 2011). When the Forestry Department's Chief Conservator of Forests, Musa Feika—who signed off on the export (and all previous animal exports for the past decade)—was challenged by the secretariat of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), he reportedly replied that "to every rule their [sic] is an exception" (cited in Peterson and Goodall 1993, p.110).

In 1986, 20 infant chimpanzees were shipped from Sierra Leone to Vienna to be used for medical testing by the Austrian pharmaceutical company Immuno (McGreal 2014). Immuno had developed an interest in using Sierra Leonean chimpanzees as early as 1983, when it had formulated plans to set up a medical testing station there that would conduct research on 60-80 chimpanzees. The plan, it appears, was a strategy to circumvent Austria's recent signing of CITES, which would have stymied chimpanzee imports for Immuno's research station in Vienna. Klaus Bieber, the honorary Austrian consul in Freetown and former business partner of Franz Sitter, was a central figure in negotiating an agreement with the Sierra Leone Government on behalf of Immuno, with Sitter being earmarked as the potential supplier of chimpanzees (Anonymous 1983b; Heneson 1983). Later documents revealed that Immuno was planning to provide "expensive gifts", such as chandeliers and grand pianos to Siaka Stevens to, presumably, curry favor (McGreal 2014; Young 2014).² The Sierra Leonean Government initially responded positively to the proposal, although it was evidently mindful of the potential international reaction to the enterprise (Anonymous 1983b; Heneson 1983).

At the end of his time in Sierra Leone, Teleki blew the whistle on the Immuno scheme and sent the incriminating documents to the International Primate Protection League (IPPL) (McGreal 2014). IPPL's director Shirley McGreal subsequently published a letter to the editor in the Journal of Medical Primatology criticizing the initiative (McGreal 1983; see also Moor-Jankowski 1983). A large-scale campaign against Immuno was subsequently enacted by a variety of animal rights organizations (Anonymous 1983a, 1983b, 1986). Immuno reacted aggressively, suing McGreal and many others for libel. The case was finally settled in 1989, against Immuno, and was seen as a landmark case of upholding first amendments' rights in the United States, where 'letters to the editor' were enshrined to be part of the right to free speech (Anonymous 1990, 1993; Peterson and Goodall 1993; Mukerjee 1997). Immuno never established its research facility in Sierra Leone, finally giving up on the project in the early 1990s. Franz Sitter left Sierra Leone around the same time, and Sierra Leone's role as a global supplier of medical testing chimpanzees came to an end (Kabasawa 2009; Peterson and Goodall 1993). Teleki's campaign of eliminating Sierra Leone's chimpanzee export trade had finally succeeded, nearly a decade after he had left the country.

Chimpanzee conservation activities have continued in Sierra Leone. Most prominently with the setting up of the Tacugama Chimpanzee Sanctuary near Freetown in 1995, the overall objective of which has been to rescue and provide a sanctuary for chimpanzees in Sierra Leone, as well as raising awareness about their conservation (Kabasawa et al. 2008; Kabasawa 2009). While the live chimpanzee export trade had largely ceased during the early 1990s, there was still a widespread domestic trade in chimpanzees—notably in the form of pets for expatriate workers (for example, Peace Corps volunteers) living in Sierra Leone. Interestingly, Tacugama conducted a nation-wide chimpanzee survey in 2010 (Brncic et al. 2010), the first since Teleki's 1980 survey (Teleki and Baldwin 1981). The survey results indicated that the number of chimpanzees remaining in the wild exceeded 5,500, much higher than the 1,500-2,500 estimated by Teleki in 1980 (Brncic et al. 2010). While the difference in numbers between the surveys may well have resulted from methodological dissimilarities, it nevertheless indicates that, despite ongoing challenges, Sierra Leone is home to one of the largest chimpanzee populations in West Africa. This was a particularly positive result, given Teleki's dire predictions for the future of chimpanzees in Sierra Leone in 1980 (Teleki pers. comm. 2012). While the report noted a number of challenges in regards to chimpanzee

² This is also discussed in the Austrian documentary *Unter Menschen/Redemption Possible* (2013), which focused on the plight of 40 chimpanzee survivors of the former Immuno laboratory in Austria.

conservation (hunting, land-use change, human-animal conflicts), the large-scale commercial exportation of chimpanzees was notably no longer an issue in the country.

Progress on establishing Outamba-Kilimi as a national park was also slow. Before leaving Sierra Leone, Teleki set up a partnership between the Forestry Department and the United States volunteer program The Peace Corps (Teleki pers. comm. 2012). Thus, after Teleki left Sierra Leone, a string of Peace Corps volunteers were put in charge of managing the park and securing its formal government gazettement. Financing and the organization of the resettlement for communities within the Park, however, remained a perennial issue. The park's management and infrastructure were gradually upgraded throughout the 1980s; however, funding sources dried up with the outbreak of Sierra Leone's civil war in 1991. Peace Corps volunteer Pam Seiser, who was working in the park at the time, formally became a volunteer of the Forestry Department (as The Peace Corps had left the country) to try and finalize the park's establishment. After 12 months, in 1993, however, Seiser left due to a lack of funding and the escalation of the conflict (P. Seiser pers. comm. 2012). The national park was finally (formally) declared in 1995, thanks to funding from a newly established coup d'état government in Freetown; however, it was a Pyrrhic victory as rebels would later pass through the area destroying the park's infrastructure (Squire 2001; Manson and Knight 2013; OKNP staff pers. comm. 2012). For most of the 1990s, Sierra Leone was in a state of civil war, and this proved to be a major setback for wildlife conservation programs in the country (Oates 1999). During the latter part of the 1990s, field trips by NGOs and government officials outside of Freetown became near impossible to conduct, and all field conservation activities came to a halt (Munro and van der Horst 2015).

Nevertheless, when the civil war ended in 2001, conservation programs returned with gusto in Sierra Leone. Facilities have now been rebuilt in Outamba-Kilimi, and it has been formally reopened as a national park and tourist site. A recent guide book noting "If you've ever dreamed about waking up to the patter of monkey pee on your tent, ... then the country's oldest national park is for you ... In Outamba, a sighting or two of hippos, chimps and monkeys is pretty much guaranteed" (Manson and Knight 2013; p.261). USAID and the US Forest Service program are also currently funding a large-scale conservation initiative in the Outamba-Kilimi National Park region (USAID and US Forestry Service 2012).

After years of challenges and setbacks, Teleki's opportunistic negotiations with Siaka Stevens in the early 1980s, finally resulted in the gazettement of the country's first national park. Conservationists have built upon this achievement and Sierra Leone now has two more national parks—the Gola Forest National Park created in 2010 in the east of the country, and the Western Area Peninsula National Park, created in 2013 near the capital city of Freetown.

Conclusion

Geza Teleki's time in Sierra Leone developing wildlife conservation initiatives, provides some interesting reflection for counterfactual histories. Would Outamba-Kilimi exist as a national park if Teleki had not been able to appeal to Siaka Stevens' hubris with the approaching OUA summit in Freetown? Would Immuno have succeeded in setting up a chimpanzee testing station in Sierra Leone if Geza Teleki had not blown the whistle early on regarding their escapades? Whatever, Teleki certainly left his mark in Sierra Leone, providing a critical foundation for future wildlife conservation activities in the small West African nation. From capricious negotiations with the presidential dictator Siaka Stevens to theurgical conflicts with local communities, besides affrays with wildlife exporters, he helped to carve out a nascent Sierra Leonean wildlife conservation movement.

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Primates as Flagships for Conserving Biodiversity and Parks in Indonesia: Lessons Learned from West Java and North Sumatra

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Abstract: Conservation International's Indonesia field program has carried out three conservation awareness programs; two are still running, while one was discontinued due to lack of funding. These conservation education programs are part of a long-term plan to prioritize large-scale efforts to conserve biodiversity in Indonesia by pulling together various stakeholders and partners. Environmental education programs can be sustained through partnerships with local NGOs, the government, universities, the private sector and donors. Successes with regard to the conservation of flagship species have been notable in some areas. The Bodogol Conservation Education Center, for example, has focused on the Javan gibbon (*Hylobates moloch*) and the Javan eagle (*Nisaetus bartelsi*), while the Sumatran orangutan (*Pongo abelii*) was used as a flagship species in the education programs at the Sibolangit Interpretive Center. Discontinuation of the Sibolangit Interpretive Center occurred due to a lack of donor support, as has been the case for many conservation education programs in Indonesia. Nationwide, few public awareness programs that focus on species have survived and been proven effective without relying on donors. A key to the success of the surviving programs is engagement with a variety of partners that provide diverse skills, funding opportunities, and resources.

Keywords: Awareness programs, conserving biodiversity and parks, Indonesia, primates

Introduction

Historically, conservation awareness has mostly been embedded in environmental education at the primary, secondary and tertiary levels of the formal education system, and in extra-curricular activities for children and adult education programs. These activities use any type of education material about nature, wildlife and the environment with the underlying goal of achieving an appreciation for and understanding of nature, with participation in activities related to its protection. The aim of these programs is to increase awareness and alter behavior to contribute to conservation and decrease environmental destruction resulting from human practices. Brown (1988) believes that only a handful of concerned scientists and environmentalists are actively engaged in the race to preserve our plant and animal life, and if he is right, we need to increase the number of people expressing concern and working on this issue. Although conservation education will not solve all environmental problems alone, effective education and communication programs are a prerequisite for better

natural resource management and, ultimately, for safeguarding the biosphere on which we all depend (Jacobson 1995).

Indonesian environmental education programs began in the late 1960s, mostly in schools, and gained momentum when the Government of Indonesia established the Ministry of the Environment in the early 1970s. Initiatives to educate Indonesians about the environment have mostly focused on curricula, biology books and related activities, such as nature clubs, at a number of universities. Non-governmental organizations (NGOs) have played a significant role, either by developing conservation centers in or near parks or by proactively working with schools to develop the necessary biodiversity conservation content for their curricula (Indrawan *et al.* 2007; Supriatna 2008).

Although public environmental education is not a new idea, it has previously only had a small-scale and short-term impact in Indonesia. The oldest environmental education facility is the Seloliman Forest Center in East Java, which brings together students, educators, farmers, governments, businesses, women's groups and the general public to learn

about the environment. Courses at Seloliman have included seminars to promote the integration of environmental education into school curricula and workshops for local villagers to learn skills for environmentally friendly living. This center is the oldest in Indonesia and has received many awards for successfully educating a wide range of stakeholders in environmental issues.

In 1995, World Wildlife Fund Indonesia created an environmental awareness program that departed from other initiatives of this sort with a special project that included cars equipped with films, and flyers for the school children, communities and stakeholders in forested areas, such as national parks and other protected areas (WWF 2014). Conservation International (CI) initiated similar programs in three locations in the early 1990s. The first was in the Gunung Gede Pangrango National Park (GGPNP) near Bogor, West Java, which is south of Jakarta, the capital city of Indonesia. The second was the Sibolangit Interpretive Center, established in North Sumatra Province as an anchor for conserving parks and biodiversity over large areas, such as the Leuser Ecosystem (2.3 million ha). The third program was located in the marine and coastal areas of Raja Ampat in West Papua. This program continues to this day and uses a large ship called "Kalabia," which means "shark" in the local language, as a mobile classroom.

In this paper, we review two conservation awareness initiatives of Conservation International that have focused on educating the communities living in forested areas around parks. Both used wildlife species as flagships: Bodogol in GGPNP in West Java; and the Sibolangit Interpretive Center in the Sibolangit Nature Reserve of North Sumatra. Both were successful for a while, but only Bodogol in south-west Java continues today. We describe the development and activities of these programs and draw lessons for future environmental education and awareness programs in Indonesia.

Bodogol Conservation Awareness Program at GGPNP

GGPNP, in West Java, was established in 1980. It was one of the first national parks in Indonesia and declared one of its six UNESCO Biosphere Reserves (Wardojo 1997). GGPNP is a 21,975-ha montane forest located around Jakarta, Bogor and Bandung in West Java, the most densely populated part of Indonesia—approximately 35 million people live around the park. The park is a 90-minute drive from Jakarta, and provides critical habitat for the endemic and Critically Endangered Javan eagle (*Nisaetus bartelsi*), the Javan grizzled leaf monkey (*Presbytis comata*), the Javan gibbon (*Hylobates moloch*) and the Javan leopard (*Panthera pardus melas*) (Supriatna 2006).

The park lies at the core of a 100,000-ha water catchment that includes the neighboring mountains of Halimun and Salak. The value of the water in this region is approximately US\$100 million/year after it is collected and sold for the consumption of approximately 20 million people in 144 villages

and five nearby cities, including Jakarta (Conservation International Indonesia 2009).

Since 1994, the national park, with the aid of CI, has been developing a consortium to promote a collaborative approach toward biodiversity conservation, education and awareness. The principal agencies are CI, the Agency for Forest Protection and Nature Conservation (PHKA) that is the part of the Ministry of Forestry that oversees the GGPNP, and the Alam Mitra Indonesia Foundation (ALAMI). The consortium also includes the University of Indonesia, the private sector, the local government, and local communities. The University of Indonesia established a research station adjacent to the conservation education facilities. Easy highway access from three major cities: Jakarta, Bogor, and Bandung make this the most frequently visited national park in Indonesia. The education center is located on the slopes of Mt Pangrango, approximately 800 m above sea level, and provides a cool and comfortable retreat from the hot, humid environment of the lower surrounding areas.

The numerous partners in the consortium have worked together to establish a range of programs to safeguard the ecosystems of the park. Major accomplishments have been the establishment of a biodiversity conservation education center, the university research station, and the Javan Gibbon Rehabilitation Center. Since 1998, the consortium members have been developing and implementing the awareness and education program as one of their conservation tools. The program set up a separate entrance from the main gate to the GGPNP to facilitate access to visitors interested in nature education. This entrance is closer to Jakarta than is the main gate and allows visitors to avoid the weekend traffic congestion found in the park. The facilities at this alternative gateway promote experiential education and allow visitors to spend several days in the center.

The alternative, informal education program at the Bodogol Conservation Education Center was designed to provide target groups with the opportunity to explore and directly experience the tropical rainforest and its surroundings. The theme of the program is "Revealing the Secrets of the Rainforest," and the educational content is classified under various topics, including "The Forest, the Food Supplier," "The Forest, the Drug Store," and "Life under a Canopy." The conservation education and awareness program has been designed to match the varied characteristics of the visitor groups, with an emphasis on providing first-hand experience exploring the tropical rainforest. The methods used to deliver the information on nature conservation issues are set up to be fun and interactive, to encourage curiosity and creativity, as well as positive and active participation.

The program also targets women, especially those living in the park or its surrounding areas, as well as members of government, particularly the staff of the Ministry of Forestry and Regional Planning. Training courses for teachers, local rangers, and government officials are held at the park. The education program also targets children from the surrounding urban and rural areas through the Nature Kid Program, and

conservation students and scientific professionals, and other interested members of the public and Indonesian business executives.

Most activities (75%) are conducted outdoors and focus on providing visitors with a first-hand experience of nature using their senses. Guided classroom activities also make up a part of the program. Other sessions (25%) are focused on introducing visitors to the forest and providing them with information about life in the forest. The outdoor activities primarily involve guided walks (including crossing a canopy walkway), nature games, and discussions. Participants are divided into small groups, usually with a maximum of six people, and are accompanied by a facilitator.

This national park is among the most frequently visited in Indonesia. Overall, 35% of the visitors are students but, from 1998 to 2013, students comprised 66.5% of the visitors to the Bodogol Conservation Education and Awareness Center

(Fig. 1). During this time, more than 50,000 people visited the center, including local school children, families, community groups, decision makers and corporate executives. Overall, the hope is that students will increase their curiosity and enhance their sense of biophilia.

The facilities that have been established since 1998 include a 100-m canopy bridge and walkway, one classroom, two furnished dormitories of 40 bunk beds each, a kitchen and restaurant, a gazebo, a park guide house, a volunteer house, display rooms and 2 km of forest tracks with scenic outlooks that include information on the park's biodiversity, ecosystems, and topography, and records their distance from the main gate (Figs. 2–5).

The Center also offers guided nature walks, lectures and training courses. A modest research center provides laboratory space and accommodations for visiting researchers at the following costs: one-day visit (including a program +

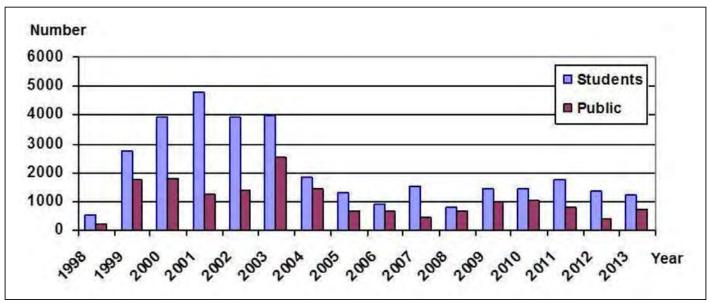


Figure 1. Number of visitors at the Bodogol Conservation Education Center each year.



Figures 2 and 3. The Bodogol Conservation Education Center (Photos © Conservation International).

ticket + insurance + guide + welcome drink) plus the canopy bridge or the Cikaweni waterfall (3–4 hours) for \$3.5 (general public) or \$2.5 (student), and for both the canopy bridge and the Cikaweni waterfall (4–6 hours) for \$5 (public) or \$3 (student). The Adventure + the canopy bridge (4–6 hours) costs approximately \$5 (public) or \$3.5 (student), while visiting the Cipadaranten waterfall (6–7 hours for a minimum of 5 people) costs \$6 (public) or \$4 (student).

There are also several packages for multiple-day visits that include program fees, tickets, insurance, interpreters, accommodation, welcome drinks, meals, and transportation. Costs range from \$20 to \$50 for one person for research tourism, family gatherings, backcountry fun, family camping, and other packages. The programs also provide benefits for the communities around the park, such as employment for field staff and interpreters and income from meal provision, local motorcycle transportation (*ojek*) and jeep rental.

From 2003 to 2007, with support from the Ford Motor Company in Jakarta, the consortium ran a mobile unit that visited hundreds of schools and thousands of students surrounding the park. The car was called "Molly and Telsi" and

symbolized two flagship animals; Molly, a Javan gibbon (*Hylobates moloch*), and Telsi, a Javan eagle (*Nisaetus bartelsi*). The car was equipped to show documentary movies and host a talk show for school children and people in the villages (Figs. 6 and 7). More than 40,000 people were visited using this unit.

Sibolangit Interpretive Center, North Sumatra

From 2001–2004, with funding from the Critical Ecosystem Partnership Fund (CEPF) and in partnership with the local office of the Ministry of Forestry, CI developed the Sibolangit Interpretive Center, located approximately a 1-hour drive from Medan toward Berastagi. The Center used the Sumatran orangutan (*Pongo abelii*) as its "flagship" species to increase public awareness about natural resource management and biodiversity conservation (Figs. 8 and 9). The Center was situated on the main road between Medan and Lake Toba in central North Sumatra near a large lake formed by the eruption of a super volcano. It focused on conservation education



Figures 4 and 5. Activities at the Bodogol Conservation Education Center (Photos © Conservation International).



Figures 6 and 7. The vehicle used to visit villages and schools (Photos © Conservation International).

and raising public awareness in the communities surrounding Gunung Leuser National Park (Perbatakusuma *et al.* 2009).

The center's staff were supported by volunteers from the surrounding communities, all of whom had undergone intensive training in nature interpretation. To reach audiences that otherwise might not have had the opportunity to learn about orangutan conservation, CI also operated the Orangutan Mobile Education Unit, which took the conservation message beyond the gates of Sibolangit to remote areas. These areas included villages of refugees from the Aceh Tsunami of December 2004 that had been created within the National Park (the second phase of program development; see Table 1).

Additional funding from USAID and a private donor was secured from 2005–2007 that allowed the Mobile Unit to expand its coverage to West Batang Toru. The Mobile Unit travelled to remote villages and camped out for 3–4 days at a time with regular return visits throughout the year. During visits, the CI team conducted informal learning sessions that ranged from school visits and puppet shows to interactive games and daytime forest walks. The Mobile Unit was warmly received by local communities and was very effective

in raising awareness among its target audiences. It reached villages and refugee camps in regencies in North Sumatra, and hundreds of people attended each session, particularly a popular, evening "orangutan film series" (Figs. 10 and 11).

The Mobile Education Unit was an integral part of the conservation education work in North Sumatra, and it also provided an important entry point for reaching local decision makers. Interpreters play a very important role in conservation education throughout the world, and through them, the public comes to understand nature and its role in supporting their livelihoods. Interpreters have the skill to communicate and translate the technical facets of the environment and its interactions in non-scientific terms in a clear and comprehensible manner. Good interpreters are as such a key component of successful conservation education programs. The training materials for interpreters include the basics of ecology for nature guides or interpreters, conservation games, the basics of nature interpretation, communication for nature guides and interpreters, the identification of the flora and fauna, jungle survival, and practice in the field.



Figures 8 and 9. Activities at the Sibolangit Interpretive Education Center (Photos © Conservation International).



Figures 10 and 11. Vehicles used to visit villages and schools (Photos © Conservation International).

As part of developing the education and awareness program, CI assessed the level of knowledge about orangutan conservation in the area surrounding Gunung Leuser National Park. Surveys were undertaken to evaluate the knowledge level, attitudes, and behaviors of the community to provide a foundation for developing a targeted campaign strategy. The surveys were conducted in three sub-districts (Bohorok, Sibolangit, and Tiga Lingga) that border or are near to orangutan habitats. The total number of respondents was 360 people, 48 of whom were the formal and informal leaders of their communities. Another assessment was specifically designed to evaluate the knowledge, attitudes, and behaviors of the decision makers (Perbatakusuma *et al.* 2009).

The survey results suggested that the communities in the sub-district of Tiga Lingga had the lowest level of knowledge about forests, orangutans, and the relationship between the two. In most of the study areas, the decline in clean water (both availability and quality) was the most important concern for the people interviewed. Most of the respondents identified their immediate welfare as their first priority, with forest destruction as a lesser concern.

Based on the responses from the target groups, three categories of educational activities were developed. The first specifically targeted adult members of the general public, including the refugees in the park. It included the creation of illustrated informational materials in the form of fact sheets and posters, the production of sermon sheets, the development of information boards for the local café, and movie sessions and discussions. The sermon sheets were pages with information on the environment and biodiversity conservation, which were developed by the programs in collaboration with the priests, and were to be given during Sunday prayer. In addition, the awareness center and the mobile unit staff also collaborated with partners to produce and distribute additional materials, such as Video News Releases (VNR), posters, t-shirts and a variety of souvenirs.

The second category specifically targeted decision makers, and included a series of meetings and visits. The targeted decision makers included the heads of local governments, members of parliament, forestry officials and members of other institutions bordering the orangutan habitats.

Table 1. Comparison of the two conservation education programs initiated by Conservation International in Indonesia.

Products	Bodogol	Sibolangit		
Location	Gunung Gede Pangrango National Park	Sibolangit Tourism park, Leuser National Park		
Target audiences	Communities around the park, visiting students, paying visitors, family gatherings, and people from the cities of Bogor, Sukabumi, Bandung, and Jakarta (the capital city of Indonesia)	Communities around the park and students from Sibolangit and Medan (the capital of North Sumatra)		
Partner organizations	The national park, CI, local NGOs, the private sector	The Conservation Office (BKSDA), CI, local NGOs, USAID		
Outreach	Both at the education center and through communities surrounding the park	Through the interpretative center and villagers around the orang- utan habitat, a radio talk show series discussing conservation and other related topics, radio spots and public service announce- ments about conservation		
Flagship species	Javan gibbon and Javan eagle	Sumatran orangutan		
Equipment	Digital film documentation and work with Muslim boarding school leaders	Digital and film documentation and work with church leaders		
Infrastructure/ vehicles	In the park: Bodogol Conservation Education Center (2 rooms with 40 bunk beds, 1 class room, 1 volunteer house, 1 staff house, guard house, 2 gazebos, 1 restaurant, 1 canopy bridge, and 2 km of trails)	In the park: Sibolangit Interpretive Center (1 office house, 1.5 loof trails, and several gazebos)		
	Outside the park: travel from school to school around the park, including the Islamic boarding school, villages, etc., in an SUV donated by Ford Motor Company	Outside the park: travel in an SUV to visit villages, schools, churches and mosques		
Funding	Collaborative partnerships (park budget, local and international companies, ticket sales, and program packages), the Keidaren Foundation from Japan, Mattel, and entrance fees and program packages	CEPF (Critical Ecosystem Partnership Fund) and USAID		
Educators	CI staff, in collaboration with the University of Indonesia, volunteers from NGOs and the park authorities, developed education modules, flyers and digital information	CI staff and, occasionally, park rangers		
Duration	1998 to present	2001–2007		
Tag lines or Programs	"Reveal the Secrets of the Rainforest," "The Forest, the Food Supplier," "The Forest, the Drug Store," and "Life under a Canopy"	"Save the Orangutan"		

Lessons Learned from Conservation Education and Awareness Programs

The CI Indonesia conservation education and awareness programs are summarized in Table 1. The two programs have many similarities in terms of their backgrounds, aims and methods. Both successfully used flagship species to reach larger audiences and attract more donors. Only the funding models differed.

The Bodogol Conservation Education and Awareness Center has successfully moved towards financial sustainability, except for the mobile unit that educated school children. This latter program has now been terminated due to insufficient funds for its operation and maintenance (Fig. 12).

The Sibolangit Center, which depended on donors rather than income from visitors and participants in its programs, was terminated in 2007 after CI handed it over to a local NGO. Unfortunately, the local NGO was unable to raise enough funding to sustain the education program.

From our review of these two programs, it seems that increasing public awareness of the important environmental services (for example, watershed protection and erosion control) provided by forests was a key component in stopping or slowing illegal logging and, ultimately, conserving orangutans and the Javan gibbon. Most of the programs offered by both centers promoted the idea of ecosystem services. In addition, appreciating how the survival of orangutans in Sumatra and of Javan gibbons and Javan eagles in Java are linked to the forests in which they live enabled communities and decision makers to understand the importance of reducing further habitat loss through the cessation of logging and/or the restoration of habitat, as well as by providing alternative livelihood opportunities for local communities.

A number of educational methods were used, including fact sheets, posters, displays, and power point presentations, along with several editions of sermon sheets to promote the importance of protecting species and nature from the perspectives of both Islam and Christianity. All of these awareness activities were preceded by an awareness needs assessment of the general public (including refugees in the case of Sumatra) and key decision makers.

Why were flagship species used? These species act as an umbrella for all other forest species. In Sumatra, many communities already knew that the habitat of the Sumatran orangutan had decreased rapidly due to habitat conversion for commercial and subsistence agriculture, logging, open-pit mining, forest fires, infrastructure development, local encroachment and many other factors. Sumatran forests are undergoing the highest rate of conversion in the world (Supriatna *et al.* 2002; Wich *et al.* 2008; Singleton *et al.* 2009), causing a loss of orangutan habitat.

The story of the Javan gibbon and Javan eagle is different. Habitat has certainly been lost for the same reasons as in Sumatra, but, currently, the main culprits threatening these species are the poachers taking their young to be sold as pets. Populations of both species have decreased significantly in the wild with no more than 5,000 individuals of the Javan gibbon (Supriatna 2006; Supriatna *et al.* 2010) and only a few hundred Javan eagles (Whitten and Soeriaatmadja 1999) remaining.

Mangunjaya (2002) recorded that the perceptions of biodiversity among middle school students around the Gunung Gede and Gunung Pangrango national parks changed after some of them had been visited by the mobile unit team. The perceptions of the significance of biodiversity among the students could be broken down into the following categories: esthetic (27%), moralistic (22%), humanistic (19%), scientific (13%), naturalistic (6%), utilitarian (4%), dominionistic (3%) and symbolistic (2%). The high scores for esthetic, moralistic and humanistic values reflect certain societal values. The esthetic value indicated an attraction to the beauty, equality, symmetry and love of nature, while the moralistic value shows a spiritual closeness with nature, indicating that people feel a need to protect and understand it (Kellert 2002).

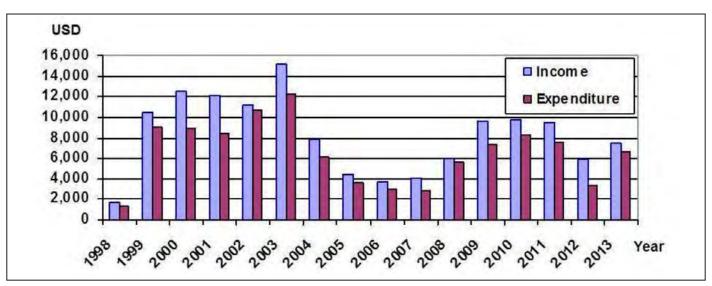


Figure 12. Income and expenditures at the Bodogol Conservation Education Center each year.

Marketing strategies, such as mass media advertising, are also extremely effective at raising public awareness and disseminating at least a small set of important facts to many people at a relatively small investment per person. Although mass media advertising campaigns can never replace an educational curriculum, they can target other important audiences and affect decision makers and other community leaders by raising awareness of issues that would otherwise not be as widely recognized. Many donors have improved protected area conservation efforts by promoting pride in endemic Indonesian biodiversity and concern over its future (Supriatna 2008).

Discussion

Ultimately, efforts to conserve biodiversity must succeed at the community level, which is where the ultimate measure of the effectiveness of conservation efforts will be felt. Alliances between civil society, communities, the private sector, and government are powerful tools to create support for environmental education and understanding. Creating alliances requires building awareness and creating incentives for people to support conservation efforts. The creation of these alliances and the dissemination of information to residents living near parks, decision makers, and participating communities have been used by CI in Indonesia in the two examples reviewed here. These conservation education programs have been successful in helping people understand the importance of ecosystems, the species in them, and their fundamental role in supporting livelihoods in West Java and North Sumatra. Public interest in the wildlife, especially charismatic species, such as orangutans and gibbons, among the villagers surrounding the parks is historically high, and has recently been reinforced by several animal programs on television.

Conservation education and awareness focused on flagship species is not new, but combining this strategy with a range of tools, as in these two examples, has been largely successful. In the case of the Bodogol Conservation Education and Awareness Center, this approach has resulted in a sustainable financing mechanism. The different models show that conservation education will ultimately be successful only if it is supported, now and in the future, with sufficient funding, either through donations or through a financial model that raises funds from visitors and ecotourists, or a combination of both.

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