

The Crisis of the Critically Endangered Greater Bamboo Lemur (*Prolemur simus*)

Authors: Wright, Patricia C., Johnson, Steig E., Irwin, Mitchell T., Jacobs, Rachel, Schlichting, Peter, et al.

Source: Primate Conservation, 23(1) : 5-17

Published By: Conservation International

URL: <https://doi.org/10.1896/052.023.0102>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The Crisis of the Critically Endangered Greater Bamboo Lemur (*Prolemur simus*)

Patricia C. Wright^{1,2,3}, Steig E. Johnson^{2,4}, Mitchell T. Irwin⁵, Rachel Jacobs^{1,2}, Peter Schlichting^{1,2},
Shawn Lehman⁶, Edward E. Louis Jr.⁷, Summer J. Arrigo-Nelson^{2,8}, Jean-Luc Raharison¹⁰,
Radoniana R. Rafalirarison^{2,9}, Vololontiana Razafindratsita¹¹, Jonah Ratsimbazafy^{9,12},
Félix J. Ratelolahy², Rainer Dolch¹³ and Chia Tan¹⁴

¹Department of Anthropology, Stony Brook University, Stony Brook, NY, USA

²Centre ValBio, Ranomafana, Madagascar

³University of Helsinki, Finland

⁴Department of Anthropology, University of Calgary, Calgary, AB, Canada

⁵Department of Biology, McGill University, Montreal, QC, Canada

⁶Department of Anthropology, University of Toronto, Toronto, ON, Canada

⁷Center for Conservation and Research, Henry Doorly Zoo, Omaha, Nebraska, USA

⁸Department of Anthropology, Notre Dame University, Indiana, USA

⁹Department of Paleontology and Biological Anthropology, University of Antananarivo, Antananarivo, Madagascar

¹⁰Department of Animal Biology, University of Antananarivo, Antananarivo, Madagascar

¹¹Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux, Antananarivo, Madagascar

¹²Durrell Wildlife Conservation Trust, Antananarivo, Madagascar

¹³Mitsinjo Project, Andasibe, Madagascar

¹⁴San Diego Zoological Society, San Diego, California, USA

Abstract: *Prolemur simus* (the greater bamboo lemur) is the most abundant lemur in the northern subfossil sites of Madagascar. Living populations still persist, but in low numbers within a diminished range, making it one of the most critically endangered lemurs. Over the past twenty years scientists have searched the south- and central-eastern rain forests of Madagascar. Despite surveys that encompass over 500 km², less than 75 animals have been found, with a recent total count of 60. More encouraging is that in 2007 two new sites containing *P. simus* were found: Mahasoan an unprotected 150 ha fragment east of the Ranomafana/Andringitra corridor (17 *P. simus*), and Torotorofotsy, a RAMSAR site near Andasibe (~16 *P. simus*). *Prolemur simus* is a bamboo specialist with a patchy geographic distribution, which may be driven by the distribution of one or two bamboo species. Home ranges are large, group size has been observed to be from four to 26 individuals, and localities may be spaced hundreds of kilometers apart. Ranomafana National Park contains the only fully habituated group, and there are a total of three groups known in the park. We make recommendations for conservation action for these populations of *P. simus*. If immediate action is taken, we may be able to prevent the extinction of this species within the next decades.

Key Words: Population surveys, greater bamboo lemur, *Prolemur simus*, Ranomafana National Park, Madagascar, Mahasoan, Torotorofotsy

Introduction

The greater bamboo lemur (*Prolemur simus*), previously known as *Haplemur simus* (see Groves, 2001), is arguably the most critically endangered lemur species in Madagascar (Ganzhorn *et al.* 1996/1997; Konstant *et al.* 2006; Mittermeier *et al.* 2006; Ganzhorn and Johnson 2007). From the subfossil record we know it was once widespread in

Madagascar, including Anjohibe and Ankarana Massif in the north, the caves of the Bemaraha Tsingy in the west, and even on the high plateau at Ampasambazimba 25 km west of Antananarivo (Godfrey and Vuillaume-Randriamanantena 1986; Simons 1997; Godfrey *et al.* 2004). It also appears to have been abundant—*P. simus* was one of the most common subfossils in the caves in the limestone massif of Ankarana Special Reserve (Simons 1997). Unfortunately, little is known

about the chronology of its decline. Using Carbon 14 dating methods, *P. simus* subfossils from Andrafiabe in the Ankarana Massif have been dated to $4,560 \pm 70$ years BP (Simons *et al.* 1995); however, none of the other subfossil sites has been dated. The measurements and dental casts of living animals (Meier 1987; Glander *et al.* 1992; Tan 1999; Yamashita *et al.* 2004) provide evidence that the subfossil specimens are similar in size and dentition to *P. simus* living today, and making it likely that the behavior and ecology would have been similar (Jernvall *et al.* 2008).

The only eyewitness accounts of living *P. simus* come from the eastern rainforest. Before the 1970s, greater bamboo lemurs were known from only two sites: a Kianjavato coffee plantation and the Vondrozo Forest (Petter *et al.* 1977; Meier and Rumpler 1987; Meier *et al.* 1987; Wright *et al.* 1987; Wright 1988). After a period of little research and much forest destruction during the 1970s and early 1980s, it was suspected that *P. simus* might be extinct (Godfrey and Vuillaume-Randriamanantena 1986). Two research teams, which arrived Madagascar in June 1986, sought to document living members of this species. A group of 12 greater bamboo lemurs was found on the edge of the Kianjavato coffee plantation (Wright *et al.* 1987), and possibly the same group ($N = 6$ individuals) was seen at the same location several months later (Meier and Rumpler 1987; Meier *et al.* 1987). A second group of 11 individuals was observed in the classified forest of Ranomafana (Meier *et al.* 1987; Wright *et al.* 1987; Wright 1988). One of the inspirations for setting aside this forest as a national park in 1991 was Ranomafana's potential for protecting populations of two rare lemur species, *Hapalemur aureus*, a recently described species (Meier *et al.* 1987), and *P. simus* (Wright 1992; Wright and Andriamihaja 2003).

Over the past 20 years research presence has increased and numerous lemur surveys have been conducted in the eastern rainforests of Madagascar. Sightings of greater bamboo lemurs, however, continue to be rare and the list of known localities has not increased appreciably (Irwin *et al.* 2005). The goal of this paper is to synthesize the results of these surveys, describe recent events concerning the attrition of the known groups, and examine data on captive *P. simus* populations. Finally, we make recommendations for conservation actions to save *P. simus* from immediate extinction.

Methods

Surveys were conducted in 69 sites over a 21-year period (1986–2007) from the Onive River in central Madagascar to the Mananara River in the south (Fig. 1). In addition, the Mitsinjo Project conducted species' incidence surveys further north, in the region of Mantadia National Park (Dolch *et al.* 2004). The study sites are rain forests, ranging in elevation from sea level to nearly 1,700 m. Surveys covered a wide range of habitat types, from isolated and degraded fragments (for example, Evendra, Sakanany) to large, relatively intact, protected areas (for example, Andringitra, Ranomafana). At each site, the forest was surveyed for lemurs, forest structure

and habitat disturbance. Although all lemur species present were recorded, results here are confined to sightings or signs of *P. simus*. Sampling effort ranged from two days, during rapid assessments in isolated forest fragments, to long-term monitoring in Ranomafana National Park and its periphery over more than 21 years. The incidence and population densities of all species of lemurs sighted during most of these surveys are presented elsewhere (Irwin *et al.* 2005). In this paper we summarize these data, and present new data from repeat surveys conducted in 2007.

As discussed above at a subset of sites ($N = 4$), forests were surveyed briefly but intensively by a minimum of two observers as part of rapid assessments of primate species richness only. At the majority of sites ($N = 65$), however, transects were established and surveyed using standard line-transect methodology (Johnson and Overdorff 1999; Struhsaker 1981; Whitesides *et al.* 1988), with existing trails used whenever possible to minimize forest disturbance (Table 1). One to four transects (1–3.5 km in length) were established in each site, and transects were walked slowly (about 1 km/hour) by 1–2 observers during each survey. Three to 26 diurnal surveys were conducted per site, with replicates generally evenly split between morning and afternoon sampling periods. During each survey, all evidence of the presence of *P. simus* (sightings, vocalizations, and feeding remains) was recorded. It should be noted that even intensive line-transect sampling in areas where *P. simus* was known to be present consistently failed to record sufficient sightings for accurate population density estimates (Irwin *et al.* 2005).

Results

Survey results

Confirmed sightings of greater bamboo lemurs occurred in only 11 of 70 survey localities with a latitudinal range of $18^{\circ}52'$ to $22^{\circ}26'S$ (Table 1, Fig. 1). Five of these sightings were in or around the protected areas of Ranomafana National Park (Miaranony, Talatahely and Ambatolahy Dimy), and Andringitra National Park (Manambolo, Camp 2). An additional unconfirmed observation occurred here (Korokoto). Another five *P. simus* sightings were in unprotected forests at Kianjavato and Karianga, and outside Evendra, Morafeno and Mahaso. Of all of these sites, Karianga, Evendra, Morafeno and Mahaso are the most degraded. Finally, *Prolemur simus* has been observed in Torotorofotsy, the only locality north of Ranomafana National Park (its southern border is near Evendra, Karianga, and Mahaso, south of Andringitra National Park and north of the Manampatrana River). The elevation range for confirmed *P. simus* sightings is considerable: 121–1,600 m, making it unlikely that the survey results have been biased due to altitudinal restrictions. Only three sites surveyed were higher (Andranofisaka and Garonina at Fandriana-Marolambo and Camp 4 at Andringitra), and three sites were lower (Manombo, Sakanany, and Mahabo) than the recorded elevational range of the species. In sum, we found *P. simus* within a relatively narrow latitudinal range but

within a broad elevational range. This species is very patchily distributed (Fig. 1), and occupies forests ranging from small, unprotected fragments to large national parks, with differing levels of anthropogenic disturbance. In the following sections, we provide further details from localities where *P. simus* has been observed.

Ranomafana National Park

Three *P. simus* groups have been seen in total at Ranomafana National Park (Wright *et al.* 1987; Wright 1988; Goodman *et al.* 2001; Grassi 2001; Irwin *et al.* 2005; Ratelolahy *et al.* 2006), with a maximum of 20 individuals confirmed. One group, that has varied from 6 to 11 individuals, has been habituated and followed since 1992 at the Talatakely site (Tan 1999). A second group of 4–6 individuals lived at Ambatolahy Dimy (just across the Namorona River, about 2 km from Talatakely. This group has been followed intermittently for

the past ten years, and continually since 2003. Its territory includes bamboo stands, both inside the national park and in the park's peripheral zone (Ratelolahy *et al.* 2006). A third group of *P. simus* was sighted briefly in 2001 in Miaranony, 15 km northeast of Talatakely and Ambatolahy Dimy, during a rapid assessment (Arrigo-Nelson and Wright 2004). In June 2007, during a 10-day resurvey, *P. simus* was not observed there, although discarded bamboo remains suggested that at least one group still exists at this site (R. Jacobs unpubl. data).

Recent observations of the two habituated *P. simus* groups at Ranomafana illustrate the vulnerability of small populations. From 1992–2004, the Talatakely group included two breeding females and two adult males. In December 2004, the two adult males disappeared, leaving a group with two adult females and two juveniles (one male and one female). It was unknown at the time if the males died from predation or

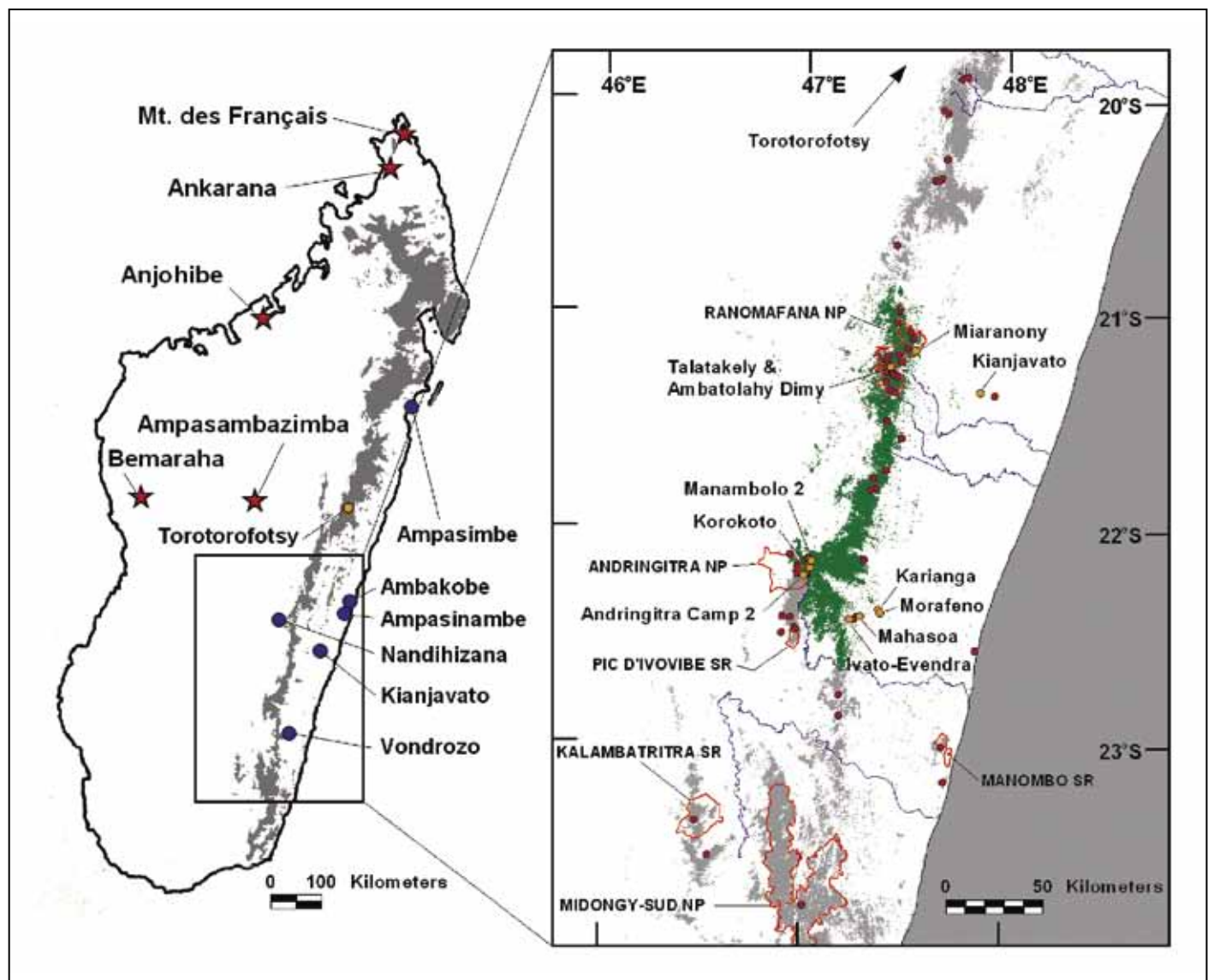


Figure 1. Past and present *P. simus* localities. Red stars are subfossil sites, blue circles are historic records, red circles are survey sites at which *P. simus* was absent, orange circles are survey sites at which *P. simus* was present. Grey represents remaining eastern rainforest (Irwin *et al.* 2005), green represents rainforest within recognized geographic range for *P. simus* based on confirmed sightings prior to 2007 (Irwin *et al.* 2005).

Table 1. Survey localities and the incidence of *P. simus*.

No.	Site	Date Surveyed	Coordinates	Elevation (m)	Investigator(s)	Source	<i>P. simus</i> present	Notes
1	Torotorofotsy	Mar–Apr 2003 Nov 2003 Jul 2007	18°52'S 48°22'E	935	R. Dolch, R. Hilgartner, J.-N. Ndrimiary, H. Randriamahazo, E. E. Louis Jr.	Dolch <i>et al.</i> (2004); E. E. Louis Jr. (unpubl.)	Yes	At least 3 social groups
2	Betsakafandrika: Jangajilo	Oct 1999	19°54'22.0"S 47°47'15.0"E	1,277	S. Lehman	Lehman & Wright (2000)	-	
3	Betsakafandrika: Bezavona	Oct–Nov 1999	19°55'02.0"S 47°45'21.0"E	1,223	S. Lehman	Lehman & Wright (2000)	-	
4	Fandriana Marolambo: Garonina	Mar 2000	20°3' 49.1"S 47°40'18.0"E	1,670	S. Lehman, J. Ratsimbazafy	Lehman <i>et al.</i> (2005)	-	
5	Fandriana Marolambo: Andranofisaka	Mar–Apr 2000	20°4'35.0"S 47°41'27.0"E	1,685	S. Lehman, J. Ratsimbazafy	Lehman <i>et al.</i> (2005)	-	
6	Kirisiasy	Jul 1999	20°17'24.0"S 47°41'24.0"E	1,200 to 1,400	M. Irwin, T. Smith	Irwin <i>et al.</i> (2000)	-	
7	Fandriana Marolambo: Korikory	Mar 2000	20°22' 58.0"S 47°39' 57.0"E	1,555	S. Lehman, J. Ratsimbazafy	Lehman <i>et al.</i> (2005)	-	
8	Fandriana Marolambo: Mananjara	Feb 2000	20°23'24.9"S 47°38'3.8"E	1,353	S. Lehman, J. Ratsimbazafy	Lehman <i>et al.</i> (2005)	-	
9	Fandriana Marolambo: Ranomena	Feb–Mar 2000	20°23'37.4"S 47°39'10.8"E	1,345	S. Lehman, J. Ratsimbazafy	Lehman <i>et al.</i> (2005)	-	
10	Vohibola III Classified Forest	Jun 2003– Dec 2005	20°41'25.9"S 47°26' 45.7"E	1,180	S. Lehman	Lehman <i>et al.</i> (2005, 2006a, 2006b)	-	
11	Marofotsy	Jun 1999	21° 00' 0.0"S 47°28'0.0"E	1,000 to 1,200	M. Irwin, T. Smith	Irwin <i>et al.</i> (2000)	-	
12	Ranomafana NP: Ampozasaha	Oct–Nov 2004	21°3'12.1"S 47°27'26.2"E	970 to 1,213	F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
13	Ranomafana NP: Tsinjorano	May 2004 May 2005	21°5'49.0"S 47°31'21.7"E	971 to 1,273	F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
14	Ranomafana NP: Namahoaka	Jun 1999	21°7'30.0"S 47°32'18.0"E	1,100 to 1,200	M. Irwin, T. Smith	Irwin <i>et al.</i> (2000)	-	
15	Ranomafana NP: Bevoahazo	Nov–Dec 2000	21°10'6.0"S 47°30'30.0"E	1,050 to 1,250	P. C. Wright	Irwin <i>et al.</i> (2005)	-	
16	Ranomafana NP: Miaranony	Jun 2001 Jun 2007	21°10'54.0"S 47°32'48.0"E	800 to 1,100	S. Arrigo-Nelson, R. Jacobs	Arrigo-Nelson & Wright (2004), Irwin <i>et al.</i> (2005), R. Jacobs (unpubl.)	Yes	One group sighted in 2001; no groups in 2007
17	Ranomafana NP: Ranomena	Nov–Dec 2000	21°12'7.0"S 47°27'42.0"E	970	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
18	Ranomafana NP: Sahateza	May 2004	21°12'20.7"S 47°24'58.5"E	1,153 to 1,258	S. Johnson, F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
19	Ranomafana NP: Vohiparara	Nov–Dec 2003 Nov–Dec 2004	21°13'23.8"S 47°24'20.9"E	1,114 to 1,198	S. Johnson, F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
20	Ranomafana NP: Torotosy	Oct 2003	21°14'12.0"S 47°28'42.9"E	872 to 1,156	S. Johnson, F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
21	Ranomafana NP: Ambatolahy Dimy	1996–2007	21°15'7.8"S 47°25'22.6"E	905	P. C. Wright, C. Tan	C. Tan (unpubl.)	Yes	Long-term study group monitored since 2000
22	Ranomafana NP: Talatakely	1986–2007	21°15'40.2"S 47°25'9.0"E	934	P. C. Wright, C. Tan, C. Grassi, F. Ratelolahy	Meier <i>et al.</i> (1987), Wright <i>et al.</i> (1987), Grassi (2001), Tan (2000)	Yes	Long-term study group monitored since 1986
23	Ranomafana NP: Sakaroa	Oct 2002	21°15'41.4"S 47°24'7.8"E	1,074	F. Ratelolahy	F. Ratelolahy (unpubl.)	-	
24	Ranomafana NP: Ambodiriana	Feb 2003	21°16'35.4"S 47°25'47.4"E	1,121	F. Ratelolahy	F. Ratelolahy (unpubl.)	-	
25	Ranomafana NP: Manidika	May 2001	21°16'54.0"S 47°23'54.0"E	1,100 to 1,300	S. Arrigo-Nelson	Arrigo-Nelson & Wright (2004), Irwin <i>et al.</i> (2005)	-	
26	Ranomafana NP: Vatoharanana	Jul 1995 Jun–Jul 1996 Aug 1998–Aug 1999 Oct 2000	21°17'24.0"S 47°26'0.0"E	1,025	C. Grassi, S. Johnson, P. C. Wright, S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001), Grassi (2001), Johnson & Overdorff (1999)	-	

continued on next page

Table 1. continued

No.	Site	Date Surveyed	Coordinates	Elevation (m)	Investigator(s)	Source	<i>P. simus</i> present	Notes
27	Ranomafana NP: Valohoaka	Oct 2002–Dec 2003 Jan–Feb 2004 Jan–Feb 2005	21°17'48.9"S 47°26'20.4"E	827 to 1,215	F. Ratelolahy, S. Arrigo-Nelson	Johnson <i>et al.</i> (2004), Johnson <i>et al.</i> (2005), S. Arrigo-Nelson (unpubl.)	-	
28	Ranomafana NP: Marotrehoh	Dec 2000	21°18'14.0"S 47°27'42.0"E	910	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
29	Ranomafana NP: Maharira	Nov 2002	21°19'34.8"S 47°24'7.8"E	1,374	F. Ratelolahy	F. Ratelolahy (unpubl.)	-	
30	Ranomafana NP: Ambinandranfotaka	Sep–Oct 2004	21°22'1.8"S 47°25'30.6"E	628 to 1,199	F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
31	Ranomafana NP: Mangevo	Apr 2004, Apr–May 2005	21°22'31.4"S 47°26'47.7"E	690 to 1,178	S. Johnson, F. Ratelolahy	Johnson <i>et al.</i> (2005)	-	
32	Kianjavato	Winter (Jun–Aug) of 1986–1990 & 1995 Nov 1999 Jan 2000 Aug 2000 Apr–May 2002 Jun–Jul 2007	21°22'31.0"S 47°51'55.0"E	121 to 235	P. C. Wright, J. Ratsimbazafy, E. E. Louis Jr., R. Jacobs	Louis Jr. <i>et al.</i> (2005), E. E. Louis Jr. (unpubl.), P. C. Wright (unpubl.), R. Jacobs (unpubl.)	Yes	Wright surveys located groups of 6–8 individuals; Jacobs located ≥2 groups with ≥7 individuals
33	Vatovavy	Winter (Jun–Aug) of 1986–1990 & 1995 Jan 2000 May 2002	21°23'18.0"S 47°56'24.0"E	175	P. C. Wright, J. Ratsimbazafy, E. E. Louis Jr.	Louis Jr. <i>et al.</i> (2005), E. E. Louis Jr. (unpubl.), P. C. Wright (unpubl.)	-	
34	Andrambovato	Oct 2000	21°30'42.0"S 47°24'36.0"E	1,075	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
35	Tolongoina: Mandriandry	Oct 2000	21°35'30.0"S 47°29'6.0"E	750	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
36	Ambantofotsy: Ambahaka	Oct–Nov 2000	21°44'12.0"S 47°24'30.0"E	750	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
37	Vinantelo	Oct 2000	21°46'36.0"S 47°20'48.0"E	1,100	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
38	Ikongo: Ambatambe	Nov 2000	21°49'18.0"S 47°21'30.0"E	625	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
39	Ikongo: Ankopakopaka	Nov 2000	21°49'42.0"S 47°20'18.0"E	645	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
40	Andringitra NP: Imitso	Aug–Sep 2000	22°8'0.0"S 46°56'0.0"E	1,500	S. Johnson, S. Razafimandimby	Johnson (2002)	-	
41	Manambolo 1	Nov 1999	22°8'58.0"S 47°01'25.0"E	1,300	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	-	
42	Ankarimbelo: Sahabe	Aug 2006	22°9'25.2"S 47°18'8.4"E	683	S. Johnson, S. Martin	Johnson & Martin (unpubl.)	-	
43	Manambolo 2	Dec 1999	22°9'48.0"S E 47° 2' 30.0"	1,600	S. Goodman, V. Razafindratsita	Goodman <i>et al.</i> (2001)	Yes	
44	Andringitra NP: Camp 4	Oct 1993	22°11'39.0"S 46°58'16.0"E	1,625	E. Sterling, Ramaroson	Sterling & Ramaroson (1996)	-	
45	Andringitra NP: Korokoto	Jul 1997	22°11'44.2"S 47°01'55.6"E	850	S. Johnson	Johnson & Wyner (2000)	Yes	Calls were heard but individuals not observed; one individual found dead and strung up on trail
46	Andringitra NP: Camp 1	Sep–Oct 1993	22°13'20.0"S 47°01'29.0"E	720	E. Sterling, Ramaroson	Sterling & Ramaroson (1996)	-	
47	Andringitra NP: 'Parc'	Jun 1999– Aug 2000	22°13'20.1"S 47°01'7.3"E	725 to 900	S. Johnson	Johnson (2002)	-	
48	Andringitra NP: Ambarongy	Apr–Jul 1999	22°13'21.4"S 47°01'15.9"E	725 to 1,100	S. Johnson	Johnson (2002)	-	
49	Andringitra NP: Camp 3	Oct 1993	22°13'22.0"S 46°58'18.0"E	1,210	E. Sterling, Ramaroson	Sterling & Ramaroson (1996)	-	

continued on next page

Table 1. *continued*

No.	Site	Date Surveyed	Coordinates	Elevation (m)	Investigator(s)	Source	<i>P. simus</i> present	Notes
50	Andringitra NP: Camp 2	Oct 1993 Feb 2000	22°13'40.0"S 47°00'13.0"E	810	E. Sterling, Ramaroson, E. E. Louis Jr.	Sterling & Ramaroson (1996), E. E. Louis Jr. (unpubl.)	Yes	2 individuals sighted 3 times on transect at 810 m asl
51	Karianga	Jul 1995 Dec 1996 Nov 2000 Jul 2007	22°23'9.8"S 47°22'40.6"E	144	C. Spoegler, P. C. Wright, E. E. Louis Jr., R. Jacobs	Louis <i>et al.</i> (2006), E. E. Louis Jr. (unpubl.), P. C. Wright & C. Spoegler (unpubl.)	Yes	26 individuals counted in 1995, 18+ individuals in 1996, no sightings in 2007
52	Morafeno	Jul 2007	22°24'18.5"S 47°23'3.4"E	208	R. Jacobs	R. Jacobs (unpubl.)	Yes	At least one group with ≥ 3 individuals
53	Ambatovaky	Jul 2007	22°25'17.0"S 47°16'13.9"E	303	R. Jacobs	R. Jacobs (unpubl.)	-	
54	Mahasoa	Jul 2007	22°25'17.3"S 47°17'3.5"E	259	R. Jacobs	R. Jacobs (unpubl.)	Yes	At least one group with ≥ 17 individuals
55	Ivohibe SR: Camp 4	Nov 1997	22°25'18.0"S 46°53'54.0"E	1200	R. Rasoloarison, B. Rasolonandrasana	Rasoloarison & Rasolonandrasana (1999)	-	
56	Ivohibe SR: Camp 5	Nov 1997	22°25'36.0"S 46°56'18.0"E	900	R. Rasoloarison, B. Rasolonandrasana	Rasoloarison & Rasolonandrasana (1999)	-	
57	Evendra	Jun 1997	22°26'2.5"S 47°15'31.7"E	425	S. Johnson	Johnson & Wyner (2000)	-	
58	Ivato-Evendra Trail	Jun 1997	22°26'6.0"S 47°13'48.0"E	300	S. Johnson	Johnson & Wyner (2000)	Yes	Single individual sighted along stream outside forest fragment
59	Ivohibe SR: Camp 1	Oct 1997	22°28'12.0"S 46°57'36.0"E	900	R. Rasoloarison, B. Rasolonandrasana	Rasoloarison & Rasolonandrasana (1999)	-	
60	Ivohibe SR: Camp 2	Oct 1997	22°29'0.0"S 46°58'6.0"E	1200	R. Rasoloarison, B. Rasolonandrasana	Rasoloarison & Rasolonandrasana (1999)	-	
61	Ivohibe SR: Camp 3	Oct – Nov 1997	22°29'48.0"S 46°53'42.0"E	1575	R. Rasoloarison, B. Rasolonandrasana	Rasoloarison & Rasolonandrasana (1999)	-	
62	Sakanany	Aug 2006	22°34'20.5"S 47°51'44.8"E	18	S. Johnson, S. Martin	S. Johnson & S. Martin (unpubl.)	-	
63	Veveembe	Jun 1995 Jun 1997 May–Sep 2000	22°47'3.9"S 47°11'6.6"E	525	S. Johnson, C. Tan	Johnson & Overdorff (1999), Johnson & Wyner (2000), Johnson (2002)	-	
64	Lambohazo	Jun 1995	22°52'52.6"S 47°11'18.4"E	c. 300	S. Johnson	Johnson & Overdorff (1999)	-	
65	Manombo SR	Jun–Aug 1993 Jun–Jul 1995 Jun–Jul 1997 Feb 1999–Jul 2000 Jul 2006	23°1'30.0"S 47°42'0.0"E	25	J. Ratsimbazafy, S. Johnson, P. C. Wright, N. Rowe, S. Martin	Johnson & Overdorff (1999), Ratsimbazafy (2002), S. Johnson & S. Martin (unpubl.), P. C. Wright & N. Rowe (unpubl.)	-	
66	Mahabo	Jul 2006	23°11'10.5"S 47°43'5.7"E	18	S. Johnson, S. Martin	S. Johnson & S. Martin (unpubl.)	-	
67	Kalambatritra SR	Jun 2000	23°22'24.0"S 46°28'12.0"E	1,400 to 1,680	M. Irwin, K. Samonds	Irwin <i>et al.</i> (2001)	-	
68	Beakora	Jan–Feb 2005	23°32'13.8"S 46°32'2.4"E	1100	P. Rabeson <i>et al.</i>	Rabeson <i>et al.</i> (2006)	-	
69	Midongy du Sud NP	Jun–Aug 1993 Jul 1995 Dec 2000	23°46'0.0"S 47°1'0.0"E	1050	P. C. Wright, S. Johnson, N. Rowe	Irwin <i>et al.</i> (2005), Johnson & Overdorff (1999); P. C. Wright & N. Rowe (unpubl.)	–	

other causes, or simply emigrated. In February 2005, a census revealed that the sole adult male and the two juveniles in the Ambatolahy Dimy group had also disappeared, leaving only a solitary adult female. In the birth season, November 2005, no offspring were born to either group. It is unlikely that the males came and went during this time, as the Talatakely group is followed by research assistants five days per week and no adult male was seen after December 2004. On 3 April 2005 (beginning of the breeding season), the remaining four animals (two adult females and two juveniles) of the Talatakely group migrated across the tourist bridge that crosses the Namorona River, and Route Nationale 25 (a paved highway), into the north parcel of the park. Several days later the Talatakely group was seen with the Ambatolahy Dimy solitary female. After a week with all five individuals feeding together in the Ambatolahy Dimy territory, the Talatakely group moved about 3 km west inside the northern parcel of the park. Then on 28 May 2005, the Talatakely group re-crossed the road and the river and returned to its original territory, without a male. In June 2005, one of the natal males who had disappeared three years previously returned and rejoined the Talatakely group. The adult female, the only remaining individual in the Ambatolahy Dimy group, remains solitary in her territory. Migration of an entire social group has never been observed in any lemur species, and this temporary migration may be an adaptation to demographic stochasticity in this historically patchily-distributed species. An infant was born on 18 December 2006 to one of the adult females in the Talatakely group, and the putative father is the male who joined the group in June 2006 (Fig. 2). We suspect that the other adult female did not give birth as well, because the new male is very likely her son, although these suspected relationships have yet to be confirmed. In June 2007, the reproducing female disappeared from the group, perhaps eaten by a predator. The infant remains an active member of the group as of September 2007, and group size is now five: one adult female, one adult male,

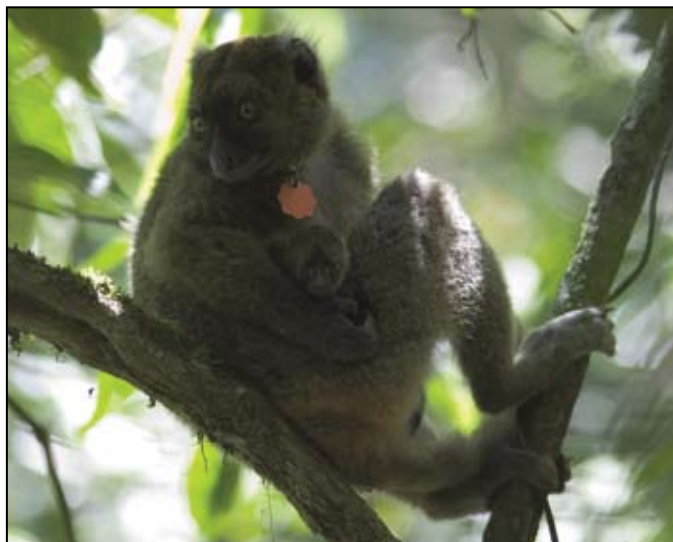


Figure 2. *Prolemur simus* mother and infant born December 18, 2007 at Talatakely, Ranomafana. Photo by J. Jernvall.

one subadult natal male, one subadult natal female and the 9-month-old infant.

Kianjavato

Since 1986, *P. simus* individuals have been observed in the bamboo patches at the edge of the Kianjavato coffee plantation, 50 km due east of Ranomafana National Park. This forest is isolated from the main eastern escarpment forest that includes Ranomafana. Two small groups were recorded in 2004 (E. E. Louis Jr. unpubl. data) and, more recently, two groups of seven individuals each were sighted in July 2007 (R. Jacobs unpubl. data). Since 1986, *P. simus* individuals captured at Kianjavato were exported to Vincennes Zoo, Mulhouse Zoo, and Cologne Zoo (Table 2).

Andringitra National Park

Sterling and Ramaroson (1996) recorded three *P. simus* sightings during surveys at Camp 2 (810 m) in October, 1993. All three sightings were of two individuals (possibly the same group each time) (Sterling and Ramaroson 1996). *Prolemur simus* was never observed, however, during 16 months of fieldwork (April 1999–August 2000) in the same area and in the adjacent Ambarongy site across the Iantara River (Johnson 2002; Irwin *et al.* 2005). A single dead individual was sighted during this period on the trail to the Korokoto site. This individual was apparently the victim of hunting, as it was strung up with rope adjacent to the trail. *Prolemur simus* vocalizations were also heard at Korokoto in July 1997 (S. E. Johnson unpubl. data). These observations suggest that *P. simus* is present but rare at Andringitra.

Evendra and Mahasoa

Evendra is a small, degraded forest south of Andringitra (Fig. 1). In June 1997, a single *P. simus* individual was observed along a stream outside Evendra, near the village of Ivato, yet no individuals were sighted inside the forest itself (S. E. Johnson and C. Spoepler unpubl. data). No individuals were sighted in this area during resurveys in July 2007. However, one large group of *P. simus* with a minimum of 17 individuals was sighted in the nearby Mahasoa agricultural

Table 2. Status in captivity and development of *Prolemur simus* ISB population 2005. (information provided by Ingrid Porton)

Participants	Status 1 Jan 2004	Births	Transfers In Out	Deaths	Status 31 Dec 2004
Asson/F	1.2	-	--	-	1.2
Besançon/F	1.1	1.0	--	-	2.1
Edinburgh/E	1.1	-	--	-	1.1
Ivoloina/M	3.1	-	--	1.0	2.1
Köln/G	1.1	-	--	-	1.1
Omega Parque	2.1	-	--	-	2.1
Port Lympne/UK	1.1	-	--	-	1.1
Paris/F	2.2	0.1	--	-	2.3
Tsimbazaza/M	1.0	-	--	-	1.0
Total	13.10 1.1		--	1.0	13.11

plantation (R. Jacobs unpubl. data; Figs. 3, 4). Virtually no forest persists in proximity to these sites (including Karianga; see below), with the landscape consisting largely of agricultural land and anthropogenic grasslands, interspersed with small, isolated bamboo patches. Remaining forests were being degraded during the study period, and are predicted to disappear completely in the near future (S. E. Johnson, E. E. Louis Jr., P. C. Wright unpubl. data).

Karianga and Morafeno

A group of 26 *P. simus* was recorded crossing a road in December 1995 in a forest fragment adjacent to Karianga village (P. C. Wright unpubl. data). Five of them were captured and housed at Ivoloïna Park, near Toamasina. In June 1996, a minimum of 18 individuals were observed in the same locality (P. C. Wright unpubl. data). Three were captured: one was brought to Tsimbazaza Botanical Garden and Zoological Park in Antananarivo and two brought to Ivoloïna Park. In 2000, six more animals were captured and delivered to Ivoloïna Park (E. E. Louis Jr. unpubl. data; see Table 2). None of the *P. simus* captured at Karianga has been exported from Madagascar.

A two-day survey was conducted in July 2007 at this site. Unfortunately, this fragment was almost entirely converted to a coffee plantation in the intervening years, and there were no additional sightings of *P. simus* there. Moreover, no vocalizations were heard and no food traces were found (R. Jacobs unpubl. data).

Another two-day survey was conducted in July 2007 near the village of Morafeno, a few kilometers from Karianga in an agricultural plantation containing large stands of giant bamboo. One group of at least three individuals was sighted there (R. Jacobs unpubl. data).

Torotorofotsy

In the Torotorofotsy marshes, 10 km northwest of Andasibe, Dolch *et al.* (2004) observed giant bamboo remains (new

shoots), and giant bamboo eaten by *P. simus* was documented in a photograph from this locality. At least three groups of *P. simus* have recently been recorded at this Ramsar site and a full description will be announced soon (E. E. Louis Jr. and R. Dolch pers. comm.). Rakotosamimanana *et al.* (2004) also described a possible sighting in nearby Maromizaha (near Andasibe). These sites are highly significant in that they substantially extend the northern range for extant populations of the species (Fig. 1). Torotorofotsy represents a habitat type (marshes) previously unrecorded for *P. simus*.

Historic vs. Present Distribution

A reasonable first-order estimate of the historic distribution of *P. simus* is a minimum convex polygon drawn around all recent sightings, subfossil sites and museum specimen sites (Fig. 1). This polygon is about 300,000 km² (half of the island). A recent estimate of current range (excluding Torotorofotsy) was 3,125 km² (Irwin *et al.* 2005), and a minimum convex polygon around all recent confirmed sightings, including Torotorofotsy (Table 1) measures about 13,000 km². Thus, *P. simus* currently occupies approximately 1 to 4% of what we believe was its former range. Current habitat areas located within protected areas total 596 km² (Dolch *et al.* 2004; Irwin *et al.* 2005), though little of this area actually seems to be occupied by *P. simus* groups due to their apparent microhabitat preferences (Arrigo-Nelson and Wright 2004). Note that even these dramatically reduced ranges are over-estimates of suitable habitat, evidenced by their highly patchy distribution across study sites within this area.

Prolemur simus in captivity

Only 39 *P. simus* individuals have been kept in captivity. As of 2007, there were 22 in seven institutions (five in Europe and two in Madagascar) (Table 2). All *P. simus* in captivity in 2007 are from Karianga and Kianjavato.

Discussion

Our results indicate a dramatic reduction in the range of *P. simus*. Furthermore, within the narrow present-day range, *P. simus* is absent from the large majority of forest habitats. Excluding surveyed sites that may be outside of the current elevational and latitudinal limits of the species, greater bamboo lemurs have been confirmed in only 12 of 69 study sites (with Torotorofotsy treated as a disjunct locality). Furthermore, the fact that only about 12 groups, totaling less than 100 individuals, have been documented in over 20 years of regional surveys is indeed alarming. It suggests that *P. simus* is currently the lemur species (and genus) with the smallest overall population size across the entire island. Alarming, several of the known localities for this species have no official protection, and even within protected areas population numbers are exceedingly low (for example, Ranomafana). Habitat loss from slash-and-burn agriculture, and use of bamboo by village residents may be further reducing the wild *P. simus* populations (Arrigo-Nelson and Wright

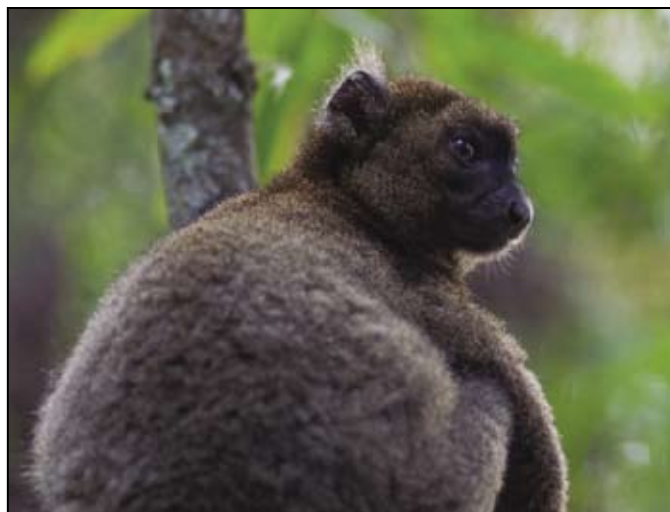


Figure 3. *Prolemur simus* adult male December, 2007 at Talatakely, Ranomafana. Photo by J. Jernvall.

2004; Wright *et al.* 2005). The long-term study of groups in Ranomafana National Park illustrates that stochastic events can deplete already small populations to critically low levels (Jernvall and Wright 1998; Wright and Jernvall 1999), suggesting that conservation planners should be aware of small population processes as an imminent cause of extinction in already-reduced and isolated subpopulations (Caughley 1994). These data corroborate other grim assessments indicating high extinction probability for *P. simus* (Konstant *et al.* 2006; Ganzhorn and Johnson 2007) and suggest that immediate action is required.

Reasons for rarity

One reason why *P. simus* is critically endangered may be its monotonous diet. Primates with a specialized diet often are at risk (Jernvall and Wright 1998; Wright and Jernvall 1999). In a long-term study of three species of bamboo lemur at Ranomafana, Tan (1999, 2000) found that the diet of greater bamboo lemurs is almost exclusively bamboo, and in fact 95% of the diet is just one species of bamboo (*Catharios-tachys madagascariensis*), with 3% being provided by other bamboo and grass species, 0.5% by fruit, and 1.5% other foods (including soil and fungi). This feeding strategy varies with

the seasons. Between July and November, *P. simus* opens the tough, woody stalks, or culms of the large bamboo by using premolars to strip the outside in order to consume the inner pith, but in December–March, it feeds on the new shoots and leaves of this same species. The group will typically feed in one small area of bamboo for a week and then move 1–2 km to a distant part of their territory to feed on another patch of *C. madagascariensis* stalks and shoots. The patchiness of this bamboo species may be one factor limiting the current distribution and population continuity of *P. simus*, as this key food species is not found in all forest microhabitats, and is apparently limited to forest near large rivers. It should be noted however, that this bamboo species was absent in Karianga, a small forest fragment where *P. simus* was observed feeding on the stalks of *Aframomum* sp., a ginger species (P. C. Wright pers. obs.). Further study of dietary breadth in other populations, therefore, is crucial to developing an understanding of this species' ecological flexibility, and eventually understanding its patchy distribution.

A second limiting factor for the distribution of *P. simus* could be the availability of drinking water. During dry months in Ranomafana National Park, *P. simus* is the only lemur species seen regularly coming to streams to drink water; other sympatric lemurs have not been observed to drink from streams, instead obtaining their water from leaves and fruits, with rainwater from foliage or tree hollows (P. C. Wright pers. obs.). This may be one explanation for the disappearance of greater bamboo lemurs from the northern part of Madagascar, as there is evidence that the north and west of Madagascar is drier now than in the past (Simons 1997; Godfrey *et al.* 2004).

Behavioral response to rarity

Recent observations of females leading a group in long-distance migration were quite notable. In other lemur species, groups maintain home ranges that change little over time, and only individual adults or subadults emigrate between groups (for example, *Propithecus edwardsi*: Pochron and Wright 2003). Because it was the mating season, and since a year without males had resulted in no offspring, we may infer that these females were searching for males, and the offspring, not yet capable of foraging independently, followed. The fact that, after presumably one month of searching, the Talatakely group did not find adult male conspecifics and returned to their original territory leads us to assume there are few if any extra-group males, and groups are spaced far apart. Although intragroup communication among individuals is frequent, there are no intergroup loud calls given by *P. simus*, as seen in sympatric *Haplemur aureus* (see Wright 1999). These observations corroborate our survey results that very few *P. simus* exist in the area surrounding the Talatakely and Ambatolahy Dimy groups at Ranomafana National Park.



Figure 4. *Prolemur simus* photographed in July, 2007 at Mahaso. Photo by P. Schlichting.

Conservation Recommendations

It is our opinion that swift action must be taken to prevent the extinction of this critically endangered species. The following are our recommendations for immediate research and conservation action.

1. Characterize the diet and microhabitat preferences of *P. simus* at known localities and use this information to identify habitats within the eastern rainforest which match known habitat preferences (i.e., are likely to contain or potentially sustain *P. simus*), and increase census efforts within these areas. The recent discovery of several groups at the Ramsar site near Torotorofotsy is very encouraging (Dolch *et al.* 2004; R. Dolch and E. E. Louis Jr. pers. comm.) and suggests surveying wetlands should be a priority.
2. Examine the levels of genetic variation over the entire population and within isolated subgroups, along with the levels of genetic relatedness within and between groups.
3. Investigate the feasibility of translocation and/or reintroduction in areas of impending habitat destruction. This would include an examination of all relevant disease and parasite issues.



Figure 5. *Prolemur simus* eating bamboo in July 2007 at Mahasoia. Photo by P. Schlichting.

4. Investigate the potential for endemic bamboo plantation and/or restocking programs in eastern forest areas to increase the area of suitable habitat and minimize future human exploitation of this resource.
5. Establish monitored protected areas in currently unprotected forests with known *P. simus* populations (Kianjavato Coffee Plantation, Ambatolahy Dimy, Mahasoia). Hire and train local people to follow these groups continually to protect them from poachers and predators.
6. Establish educational and public awareness programs in all sites where *P. simus* occurs.

Decisions need to be made in the very near future regarding a concerted effort to preserve this species. Rather than working disparately towards ill-defined goals, concerned organizations, governments, communities, and individuals need to make firm, collaborative decisions on which types of conservation strategy to pursue. Areas with known populations should immediately be gazetted as protected areas, with sufficient protection put in place. The data presented here suggest that a failure to make and act on such decisions in the immediate future may lead to the extinction of this monotypic genus.

Acknowledgments

We thank the Government of Madagascar for authorization to do research in Madagascar, especially the Association Nationale pour la Gestion de Aires Protégées (ANGAP), the Ministère de l'Environnement, des Eaux et Forêts et du Tourisme, and the Tripartite Committee (CAFF/CORE). We also thank the Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux (MICET) for their support, and the employees of ANGAP-Ranomafana National Park, the Institute for the Conservation of Tropical Environments (ICTE), and Centre ValBio for their research assistance. We appreciate the authorization of Jukka Jernvall to use his photos. Ingrid Porton and Andrea Katz are thanked for contributing the information on the captive population of *P. simus*. Anna Feistner, Jukka Jernvall and Karen Samonds provided excellent comments on the manuscript. Financial support from the David and Lucile Packard Foundation, Saint Louis Zoo's WildCare Institute, the Primate Action Fund, Primate Conservation, Inc., Nando Peretti Foundation, Earthwatch Institute and the Margot Marsh Biodiversity Foundation is gratefully acknowledged.

Literature Cited

- Arrigo-Nelson, S. J. and P. C. Wright. 2004. Census and survey results from Ranomafana National Park: new evidence for the effects of habitat preference and disturbance on the genus *Haplemur*. *Folia Primatol.* 75: 331–334.
- Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63: 215–244.

- Dolch, R., R. D. Hilgartner, J. N. Ndriamiary and Randriamahazo H. 2004. The grandmother of all bamboo lemurs: evidence for the occurrence of *Hapalemur simus* in fragmented rainforest surrounding the Torotorofotsy marshes, central eastern Madagascar. *Lemur News* 9: 24–26.
- Ganzhorn, J. U. and S. E. Johnson. 2007. Greater bamboo lemur *Prolemur simus* (Gray, 1871). In: *Primates in Peril: The World's 25 Most Endangered Primates 2004–2006*, R. A. Mittermeier *et al.* (compilers), pp.4, 21–22. *Primate Conserv.* (22): 1–40.
- Ganzhorn, J. U., S. O'Connor, O. Langrand, B. Rakotosamimanana, A. T. C. Feistner, A. Katz, Y. Rumpler and P. C. Wright. 1996/1997. The state of lemur conservation in Madagascar. *Primate Conserv.* (17): 70–86.
- Glander, K. E., P. C. Wright, P. S. Daniels and A. M. Merenlender. 1992. Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *J. Hum. Evol.* 22: 1–17.
- Godfrey, L. R., E. L. Simons, W. L. Jungers, D. D. De Blieus and P. S. Chatrath. 2004. New discovery of subfossil *Hapalemur simus*, the greater bamboo lemur in western Madagascar. *Lemur News* 9: 9–11.
- Godfrey, L. R. and M. Vuillaume-Randriamanantena. 1986. *Hapalemur simus*: endangered lemur once widespread. *Primate Conserv.* (7): 92–96.
- Goodman S. M., V. Razafindratsita, H. Schütz and R. Ratsimbazafy. 2001. Les lémuriens. In: *Inventaire Biologique du Parc National de Ranomafana et du Couloir Forestier qui la Relie au Parc National d'Andringitra*, S. M. Goodman and V. Razafindratsita (eds.), pp.231–243. CIDST, Antananarivo.
- Grassi, C. 2001. The Behavioral Ecology of *Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-bodied Prosimian Folivore. PhD dissertation, University of Texas at Austin, Austin, TX.
- Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.
- Irwin, M. T., S. E. Johnson and P. C. Wright. 2005. The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx* 39: 204–218.
- Irwin, M. T., K. E. Samonds and J. -L. Raharison. 2001. A biological inventory of the lemur community of Réserve Spéciale de Kalambatritra, south-central Madagascar. *Lemur News* 6: 24–28.
- Irwin, M. T., T. M. Smith and P. C. Wright. 2000. Census of three eastern rainforest sites north of Ranomafana National Park: preliminary results and implications for lemur conservation. *Lemur News* 5: 20–23.
- Jernvall, J. and P. C. Wright. 1998. Diversity components of impending primate extinctions. *Proc. Natl. Acad. Sci. USA* 95: 11279–11283.
- Jernvall, J., C. Gilbert and P. C. Wright 2008. Peculiar tooth homologies of the greater bamboo lemur (*Prolemur = Hapalemur simus*): When is a paracone not a paracone? In: *Elwyn Simons: A Search for Origins*, J. G. Fleagle, and C. C. Gilbert (eds.), pp. 335–342. Springer, New York.
- Johnson, S. and D. Overdorff. 1999. A census of brown lemurs (*Eulemur fulvus* spp.) in southeastern Madagascar: methods-testing and conservation implications. *Am. J. Primatol.* 47: 51–60.
- Johnson, S. and Y. Wyner. 2000. Notes on the biogeography of *E. f. albocollaris*. *Lemur News* 5: 25–28.
- Johnson, S. E. 2002. Ecology and Speciation in Brown lemurs: White-collared Lemurs (*Eulemur albocollaris*) and Hybrids (*Eulemur albocollaris* × *Eulemur fulvus rufus*) in Southeastern Madagascar. PhD dissertation, University of Texas at Austin, Austin, TX.
- Johnson S. E., P. C. Wright, T. H. Keitt, K. L. Kramer, F. J. Ratelohay, Ravalison, C. H. Holmes, W. Gordon and J. -P. Puyravaud. 2005. Predictors of local variation in lemur abundance at Ranomafana National Park, Madagascar. *Am. J. Phys. Anthropol.* Suppl. 40: 122.
- Konstant, W. R., J. U. Ganzhorn and S. E. Johnson. 2006. Greater bamboo lemur *Prolemur simus* (Gray, 1871). In: *Primates in Peril: The World's 25 Most Endangered Primates 2004–2006*, R. A. Mittermeier, C. B. Valladares-Padua., A. B. Rylands, A. A. Eudey, T. M. Butynski, J. U. Ganzhorn, R. Kormos, J. M. Aguiar and S. Walker. (compilers), pp.3, 19. *Primate Conserv.* (20): 1–28.
- Lehman, S. M., A. Rajaonson and S. Day. 2006a. Edge effects and their influence on lemur distribution and density in southeast Madagascar. *Am. J. Phys. Anthropol.* 129: 232–241.
- Lehman, S. M., A. Rajaonson and S. Day 2006b. Lemur responses to edge effects in the Vohibola III Classified Forest, Madagascar. *Am. J. Primatol.* 68: 293–299.
- Lehman, S. M., J. Ratsimbazafy, A. Rajaonson and S. Day. 2005. Decline of *Propithecus diadema edwardsi* and *Varecia variegata variegata* (Primates: Lemuridae) in south-east Madagascar. *Oryx* 40: 108–111.
- Lehman, S. M. and P. C. Wright. 2000. Preliminary study of the conservation status of lemur communities Betsakafandrika region of eastern Madagascar. *Lemur News* 5: 23–25.
- Louis, E. E., M. S. Coles, R. Andriantompohavana, J. A. Sommer, S. E. Engberg, J. R. Zaonarivelo, M. I. Mayor and R. A. Brenneman. 2006. Revision of the mouse lemurs (*Microcebus*) of Eastern Madagascar. *Int. J. Primatol.* 27: 347–389.
- Louis, E. E., J. H. Ratsimbazafy, V. R. Razakamaharao, D. J. Pierson, R. C. Barber and R. A. Brenneman. 2005. Conservation genetics of black-and-white ruffed lemurs, *Varecia variegata*, from southeastern Madagascar. *Anim. Conserv.* 8: 105–111.
- Meier, B., R. Albignac, A. Peyrieras, Y. Rumpler and P. C. Wright. 1987. A new species of *Hapalemur* (Primates) from southeast Madagascar. *Folia Primatol.* 48: 211–215.

- Meier, B. and Y. Rumpler. 1987. A preliminary survey of *Hapalemur simus* and a new species of *Hapalemur* in eastern Betsileo, Madagascar. *Primate Conserv.* (8): 40–43.
- Mittermeier, R. A., W. R. Konstant, F. Hawkins, E. E. Louis, O. Langrand, J. Ratsimbazafy, R. Rasoloarison, J. U. Ganzhorn, S. Rajaobelina, I. Tattersall and D. M. Meyers. 2006. *Lemurs of Madagascar*. Conservation International, Washington, DC.
- Petter, J.-J., R. Albignac and Y. Rumpler. 1977. Faune de Madagascar 44: Mammifères Lémuriens (Primates Prosimiens). ORSTROM/CNRS, Paris.
- Pochron, S. T. and P. C. Wright. 2003. Variability in adult group compositions of a prosimian primate. *Behav. Ecol. Sociobiol.* 54: 285–293.
- Rabeson, P., D. Randrianarisata, P. Rasabo, D. Andrianoely, G. Razafindrakoto, D. Razafindraibe, L. Rasabo and P. C. Wright. 2006. Surveys for lemurs and biodiversity in the Beakora forest southeast of Kalambatritra Reserve, Madagascar. *Lemur News* 11: 5–9.
- Rakotosamimanana, B., R. R. Ralaarison, R. C. Ralisoamalala, T. M. Rasolofoharivelo, V. Raharimanantsoa, R. M. Randrianarison, J. G. Rakotondratsimba, D. R. W. Rasolofoson, E. O. Rakotonirainy and T. M. Randriamboavonjy. 2004. Comment et pourquoi les lémuriens diurnes disparaissent peu à peu dans les forêts d'Ambato et de Moramanga (région de Moramanga) Madagascar? *Lemur News* 9: 19–24.
- Rasoloarison, R. and B. P. N. Rasolonandrasana. 1999. Les lémuriens. In: *Inventaire biologique de la réserve spéciale du pic d'Ivohibe et du couloir forestier qui la relie au Parc National d'Andringitra*, S. M. Goodman and B. P. N. Rasolonandrasana (eds.), pp.159–169. CIDST, Antananarivo, Madagascar.
- Ratelolahy, F. J., S. E. Johnson and P. C. Wright. 2006. Distribution and patchiness of endangered lemurs in the Ranomafana Rainforest of Madagascar: The crisis of the greater bamboo lemur. *Int. J. Primatol.* 27(suppl. 1): 501.
- Ratsimbazafy, H. J. 2002. On the Brink of Extinction and the Process of Recovery: Responses of Black-and-White Ruffed Lemurs (*Varecia variegata variegata*) to Disturbance in Manombo Forest, Madagascar. PhD Dissertation, State University of New York at Stony Brook, Stony Brook, NY.
- Simons, E. L. 1997. Lemurs old and new. In: *Natural Change and Human Impact in Madagascar*, S. M. Goodman and B. D. Patterson (eds.), pp.142–166. Smithsonian Institution Press, Washington, DC.
- Simons, E. L., D. A. Burney, P. S. Chatrath, L. R. Godfrey, W. L. Jungers and B. Rakotosamimanana. 1995. AMS 14C dates for extinct lemurs from caves in the Ankarana Massif, Northern Madagascar. *Quat. Res.* 43: 249–254.
- Sterling, E. J. and M. G. Ramaroson. 1996. Rapid assessment of the primate fauna of the eastern slope of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana Zool.* 85: 293–305.
- Struhsaker, T. T. 1981. Census methods for estimating densities. In: *Techniques for the Study of Primate Population Ecology*, pp.36–80. National Research Council, National Academy Press, Washington, DC.
- Tan, C. L. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. *Int. J. Primatol.* 20: 547–566.
- Tan, C. L. 2000. Behavior and Ecology of Three Sympatric Bamboo Lemur Species (Genus *Hapalemur*) in Ranomafana National Park, Madagascar. PhD dissertation, State University of New York at Stony Brook, Stony Brook, NY.
- Whitesides, G., J. F. Oates, S. Green and R. Kluberanz. 1988. Estimating primate densities from transects in a West African rain forest: a comparison of techniques. *J. Anim. Ecol.* 57: 345–367.
- Wright, P. C. 1988. Lemurs lost and found: three species of these primates are discovered alive and well and living on bamboo. *Nat. Hist.* 97: 56–60.
- Wright, P. C. 1992. Primate ecology, rainforest conservation, and economic development: building a national park in Madagascar. *Evol. Anthropol.* 1: 25–33.
- Wright, P. C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Yearb. Phys. Anthropol.* 42: 31–72.
- Wright, P. C. and B. Andriamihaja. 2003. The conservation value of long-term research: a case study from the Parc National de Ranomafana. In: *The Natural History of Madagascar*. S. M. Goodman and J. P. Benstead (eds.), pp.1485–1488. University of Chicago, Chicago.
- Wright, P. C. and J. Jernvall. 1999. The future of primate communities: A reflection of the present? In: *Primate Communities*, J. G. Fleagle, C. H. Janson and K. E. Reed (eds.), pp.295–309. Cambridge University Press, Cambridge, UK.
- Wright, P. C., P. S. Daniels, D. M. Meyers, D. J. Overdorff and J. Rabaso, J. 1987. A census and study of *Hapalemur* and *Propithecus* in southeastern Madagascar. *Primate Conserv.* (8): 84–88.
- Wright, P. C., P. Daniels, D. M. Meyers, D. J. Overdorff and J. Rabesoa. 1987. A census and study of *Hapalemur* and *Propithecus* in southeastern Madagascar. *Primate Conserv.* (8): 84–88.
- Wright, P. C., B. Andriamihaja and S. Raharimiandra. 2005. Tanala synecological relations with lemurs in southeast Madagascar. In: *Commensalism and Conflict: The Primate-Human Interface*, J. D. Paterson and J. Wallis (eds.), pp.118–145. American Society of Primatologists, Norman, OK.
- Yamashita, N., C. Tan and C. Vinyard. 2004. Crushing abilities and jaw mechanics of *Hapalemur* species in Ranomafana National Park, Madagascar. *Am. J. Phys. Anthropol.* 127: 33–45.

Authors' addresses:

Patricia C. Wright, Department of Anthropology, Stony Brook University, Stony Brook, NY, USA. E-mail: <patcwright@aol.com>.

Steig E. Johnson, Department of Anthropology, University of Calgary, Calgary, AB, Canada.

Mitchell T. Irwin, Department of Biology, McGill University, Montreal, QC, Canada.

Rachel Jacobs, Department of Anthropology, Stony Brook University, Stony Brook, NY, USA.

Peter E. Schlichting, Department of Anthropology, Stony Brook University, Stony Brook, NY, USA.

Shawn Lehman, Department of Anthropology, University of Toronto, Toronto, ON, Canada.

Edward E. Louis Jr., Center for Conservation and Research, Henry Doorly Zoo, Omaha, NE, USA.

Summer J. Arrigo-Nelson, Department of Anthropology, University of Notre Dame, IN, USA.

Radoniana R. Rafalirarison, Department of Paleontology and Anthropology, University of Antananarivo, Antananarivo, Madagascar.

Jean-Luc Raharison, Department of Animal Biology, University of Antananarivo, Antananarivo, Madagascar.

Vololontiana Razafindratsita, Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux, Antananarivo, Madagascar.

Jonah Ratsimbazafy, Durrell Wildlife Conservation Trust, Antananarivo, Madagascar.

Félix J. Ratelolahy, Centre ValBio, Ranomafana, Madagascar.

Rainer Dolch, Mitsinjo Project, Andasibe, Madagascar

Chia Tan, San Diego Zoological Society, San Diego, CA, USA.

Received for publication: September 2007

Revised: February 2008