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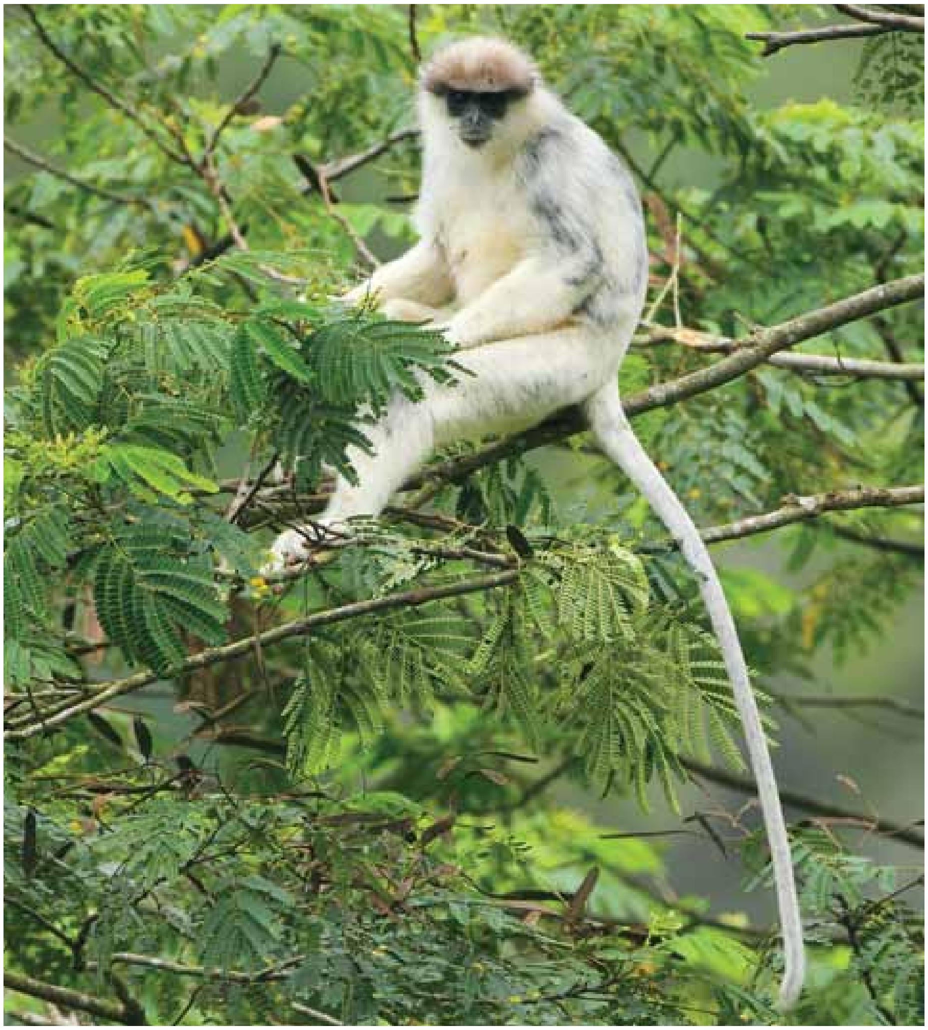

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Primate Conservation

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Front cover: A pale color morph of the purple-faced langur, *Semnopithecus vetulus vetulus*, in southwestern districts of Galle and Matara, in the wet zone of Sri Lanka. Photo by Nadika Hapuarachchi. See page 115.

This issue of *Primate Conservation* was kindly sponsored by the Margot Marsh Biodiversity Foundation, Virginia, USA, the Los Angeles Zoo, Los Angeles, California, and the Department of Anatomical Sciences of the State University of New York at Stony Brook, Stony Brook, NY, USA.

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Population Size, Distribution and Conservation Status of Howler Monkeys (*Alouatta coibensis trabeata*) and Spider Monkeys (*Ateles geoffroyi azuerensis*) on the Azuero Peninsula, Panama

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Abstract: The Azuero howler monkey, *Alouatta coibensis trabeata*, and the Azuero spider monkey, *Ateles geoffroyi azuerensis*, are endemic to the Azuero Peninsula, southwestern Panama, Central America and they are considered Critically Endangered. They are threatened by deforestation, poaching, and illegal trade. I carried out population surveys of the two subspecies from April 2001 to June 2009. The study covered potential habitats for these primates in the three provinces where they are believed to occur (Herrera, Los Santos and part of Veraguas). Surveys determined their occurrence and locations in each province. In all, 7,821 hrs were spent in survey activities. I used four methods: 1) Direct observation of presence/absence; 2) triangulations based on vocalizations; 3) strip-transect censuses, and 4) road counts. Forty-five Azuero howler monkey groups were seen and counted, totaling 452 individuals with a mean of 9.6 individuals/group, SE ±3.3 (range = 3–26). I estimate approximately 322 howler groups and *c.* 3,092 individuals remaining in the wild in the three provinces. For the Azuero spider monkey, 74 individuals in 10 sub-groups and five complete groups were counted directly, with a mean of 3.8 individuals/subgroup, SE ±0.6 (range 2–7) and a mean of 12.5 individuals/group, SE ±3.7 (range 10–22). Overall, I confirmed the existence of approximately 13 spider monkey subgroups and 145 individuals of *A. g. azuerensis* remaining in the wild in the provinces of Veraguas and Los Santos. It is already extinct in the province of Herrera. This study confirms that both subspecies are Critically Endangered. Each appears to have already experienced changes in group composition due to isolation and habitat degradation. Conservation measures based on educational awareness programs have been initiated.

Key words: *Alouatta coibensis trabeata*, *Ateles geoffroyi azuerensis*, Azuero howler monkey, Azuero spider monkey, distributions, conservation status, Azuero Peninsula, Panama

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Introduction

This is the first range-wide assessment of the distributions and populations of the Azuero howler monkey, *Alouatta coibensis trabeata*, and the Azuero spider monkey, *Ateles geoffroyi azuerensis*; endemic to the Azuero Peninsula of southwestern Panama (Froehlich and Froehlich 1987). Both are assessed as Critically Endangered on the *IUCN Red List of Threatened Species* (Cuarón *et al.* 2008). Surveys were carried out, using four conventional techniques to assess population parameters of the two subspecies. The aim was to calculate not only total numbers in Azuero but to obtain information on group characteristics, specifically their group structure, relating the findings to habitat size and other environmental variables. These two primates are among the most endangered in Panama, and the information obtained will provide a basis for the Fundación Pro-Conservación de los Primates Panameños (FCPP) and the Panama Environmental Authority (ANAM) to establish and enforce a conservation program. In this assessment I identify promising localities (e.g., villages, towns, protected areas) and primate populations for the development of long-term conservation projects and environmental education programs for local people (Jacobson *et al*. 2006). As stressed by Godfray and Crawley (2004), to improve conservation prospects of threatened wildlife in deforested regions such as the Azuero Peninsula, the remaining forests that still hold wild populations, need to be assessed to document the extent of environmental change that is taking place and responses to these changes by the endangered primate subspecies.

Methods

Study area

Azuero howler and spider monkeys are endemic to the Azuero Peninsula in the southwest of Panama. Annual average temperature is 28.1°C (range 22.5–33.7°C), and average annual rainfall is 1,410 mm/year (Navas *et al*. 2001). Azuero, encompassing the provinces of Herrera, Los Santos and the eastern part of Veraguas, is severely deforested. There is a dry season from December to April, and a rainy season from May to December (Suárez 1981). The lowlands are quite flat with small hills reaching 90 to 150 m above sea level (Méndez-Carvajal 2001). The El Montuoso Forest Reserve, at 900 m above sea level (Arcia *et al*. 2004), is in the highlands in the north, and the Cerro Hoya Natural Park (Cerro Hoya reaches 1,559 m above sea level) is in the southwest. Forests in the Azuero Peninsula remain mainly on hilltops and along rivers. The lowlands are dominated by pasture interspersed with forest patches that are connected in some areas by gallery forest and living fences. The tallest trees reach 15 to 20 m in the remnant forests and living fences that line the principal and secondary roads, delimiting the cattle ranches and pastures (Méndez-Carvajal 2001, 2008). Vegetation was classified and mapped using satellite data from GH NASA-Tele Atlas 2008 and Garmin Etrex (MapSource 6.15.4), along with information provided by the Panamanian Environmental Authority (ANAM) and the landowners. Statistical analyses were carried out using Excel, SPSS 16.0. Spearman's tests were applied to evaluate relationships between group size, forest height and the area of the habitat. The study area was divided into five regions (see Fig. 1, Table 1).

Data collection

I report here on survey data collected over nine years — 7,821 hours in the field from April 2001 to June 2009. Surveys were carried out on 121 days (10–15 days per year) (Table 2). Population densities were calculated by the number of individuals found divided by the size of each connected region; providing as such ecological densities, as indicated by Eisenberg (1979), Chapman *et al.* (1988) and Rudran *et al.* (1996).

Areas were selected on the basis of the presence of forest and information provided by the local people. Four methods were used in each survey area: presence/absence recording, strip transect, road count, and listening for calls and locating groups by triangulation. Besides seeing the primates, we recorded their presence through signs, which included smell, feces, tracks, chewed leaves, and calls (Rabinowitz 2003). Twelve strip transects were set up, each at least 1 km long, to cover the entire peninsula, following the recommendations

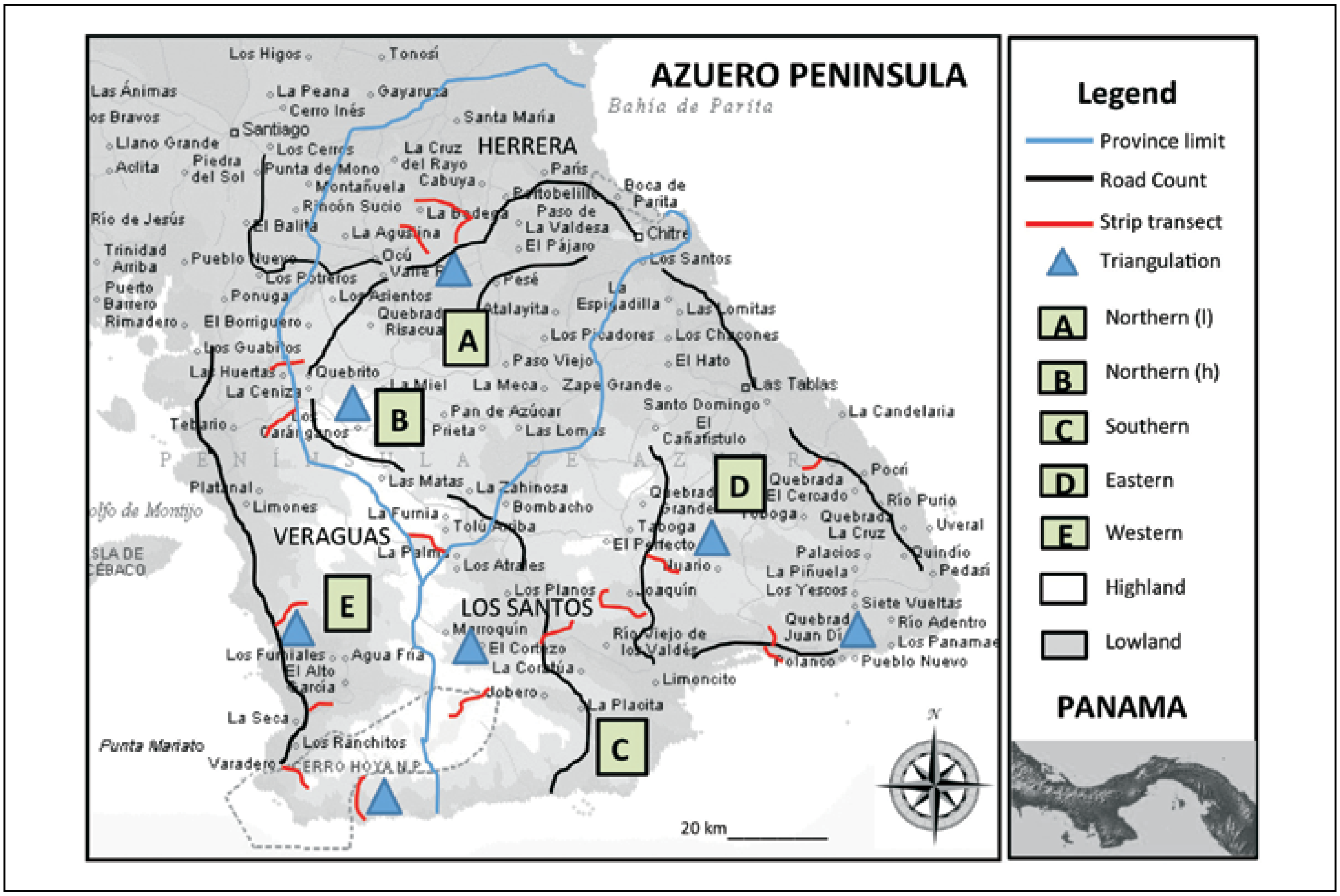

Figure 1. Study site. Location of areas where surveys have been carried out along the Azuero Peninsula.

of Ferrari (2002) and Carvalho-Oliveira *et al.* (2003) (Fig. 1). We carried out strip transects if the forest was at least 40 m wide. This method was used to survey gallery forest, living fences and patches of forest in fragments. Observations were made on foot between 08:00 and 12:00 hr and 14:00 and 18:00 hr. Speed of travel along the strip transects was 1 km/hr by foot. Eleven roads were also surveyed, averaging 26.6 km (range 18–34 km; n = 11). Each was surveyed by car twice a year; average speed was 15 km/hr.

The use of listening posts and triangulation to locate groups proved effective for howler monkeys in seven areas with isolated patches of forest (Fig. 1). Three listening posts were set up and manned from 04:30, for fixed periods in the morning, noon and late afternoon for at least three days in each area. We recorded the time and position of vocalizations using a GPS, and estimated the location of vocalizing groups using a compass-bearing and an estimated distance from the observer (Brockelman and Ali 1987; Aldrich *et al.* 2006). Whenever possible, the groups recorded were verified by direct observation later in the morning. They were counted and recounted at least twice each day while we stayed in the area. This process was repeated several times to ensure accuracy before an average group size and composition could be recorded (Milton 1992; Ferrari 2002). This method helped us to identify new groups unnoticed by our conventional strip transect method. Spider monkeys were detected with this method in previous surveys in the area of Chucantí, Darien (Méndez-Carvajal *et al.* 2010a). Black spider monkeys, *Ateles fusciceps rufiventris*, call almost every day throughout the day, and we expected the same behavior in Azuero. Azuero spider monkeys were, however, largely silent, probably because people chase them and sometimes shoot them. Azuero spider monkeys always fled when we found them, often subsequently mixing with groups of the similarly colored howler monkeys. They called so infrequently that this method proved impractical for this species in fragmented habitats.

For each group seen we recorded the group size and composition — adult male, adult female, juvenile and infant, following the classifications of Milton (1992) and Campbell and Gibson (2008). The number of groups detected was multiplied by the average group size for each area (Milton 1992). The combination of the four methods maximized our chances of detecting the groups remaining around the non-protected areas. The results from the different methods were analyzed separately but were complementary and allowed us to consolidate our information on the groups at each site.

Data Analysis

I calculated mean group size and composition for each subspecies. To estimate the total number of individuals of a subspecies present in a given area, I calculated densities as follows: Transects and Road counts: $D = N/2WL$; density (D) is found by dividing the number of individuals (N) recorded by twice the estimated detection distance (W) of the forest surveyed, multiplied by the length (L) of the transect.

For triangulation: $D = fn/A$; density (D) is found by multiplying the number of groups located by triangulation in a sampled area (N) by a correction factor for the bias that not

Table 1. Characterization of five Azuero regions divided in this study according to the provinces surveyed (see Fig. 1). Climatic and botanical information from Navas *et al.* 2001, Salazar-Allen (2001), and Arcia *et al*. 2004. Human population data from (González 2002).

Region	Coordinates	Localities	Vegetation	Highest elevation (m)	Annual rainfall (mm)	Forest cover (%)	Canopy height (m)	Temperature (ºC)	Forest cover/ Forest surveyed/ Human population
Northern (lowland)	8º00'17"N 80º41'50"W	Ocú, La Polonia, Calabazal, Llano Grande, Llano Hato, Santa Mónica, Pedregoso, Parita, Cabuya, Aguas Buenas	Secondary forest, living fences, gallery forest. Dry forest.	100	1,400	50	15	33	4% (100.5 km²)/ 42% (76.3 km²)/ 107,911
Northern (highland)	7°45'17"N 80°45'05"W	Alto del Higo, El Ñuco, Caras Pintadas, Tres Puntas, Sonadora, Chepo de Las Minas. Reserva Forestal El Montuoso (RFEM)	Secondary connected forest, pre-montane, gallery forest, living fences. Montane forest.	1000	2,500	90	25	28	
Southern (Veraguas/ Los Santos)	7º19'01"N 80º27'56"W	Restingue, Cambutal, Tembladera, Güera, Venao, Tonosí, Cañas, SE Cerro Hoya and SW Reserva la Tronosa (RFLT)	Secondary forest, gallery forest, living fences. Dry forest.	1,500	2,000	65	15	30	
Eastern (Los Santos)	7º35'14"N 80º17'51'W	Las Tablas, Oria, La Miel, El Cocal, La Palma, Tonosí and Flores	Secondary forest, living fences, gallery forest. Dry forest.	100	1,500	70	15	33	7%(168 km²)/ 39% (66.32 km²)/ 88,487
Western (South-east Veraguas)	07º22'20"N 80º51'44"W	Arenas, Quebro, Flores, Mariato, Torio, Playita, bourder of Parque Nacional Cerro Hoya	Secondary forest, living fences, gallery forest. Dry forest.	500	1,400	65	15	34	8%(250 km²)/ 36%(90 km²)/ 4,492

all groups vocalize in the same sample period (f), divided by the study area (A) (Brockelman and Ali 1987).

Azuero howler monkey analysis

To estimate of the overall density for *Alouatta coibensis trabeata*, I used results of the two most effective methods applied for this survey: triangulation and strip transects. The total number of individuals was calculated using mean group size multiplied by the number of groups detected in connected forest. Using all relevant data, we tried to estimate the number of groups existing in the more isolated areas. Total population size was calculated using the criteria of Nichols and Conroy (1996). Thus, the equation used to calculate the total population of *A. c. trabeata* was based on a modification of the Eisenberg (1979) ecological formula with a canonical estimator as following:

$$\check{N} = C/\alpha\beta$$

where C is the total number of animals, $\beta =$ Observation probability expressed as $\beta = \hat{y}/\chi$, $\hat{y}$ is the density of the incomplete population survey (Strip Transect), and χ the most accurate density of the complete survey (Triangulation); $\alpha =$ is the area sampled.

Azuero spider monkey analysis

The *A. g. azuerensis* population was estimated using two of the four methods applied for this survey. The most effective methods to detect Azuero spider monkeys were road counts and presence/absence, considering between them the presence/absence as the more complete and the road count as the less accurate method. We calculate their total population by the number of localities confirmed as "spider monkey present" and then, assuming at least one subgroup per locality, we multiplied the average subgroup size obtained by direct observations and determine the total population by the equation:

$$\check{N} = C/\alpha\beta$$

where C is the total number of animals, $\beta =$ Observation probability expressed as $\beta = \hat{y}/\chi$, where $\hat{y}$ is the density of the incomplete population survey (road counts) and the χ the most accurate density of the complete survey (presence/absence); $\alpha =$ is the area sampled.

Results

Total hours/effort invested in presence/absence recording, including informal interviews, for both species was 771.5 hours. Howler monkeys and spider monkeys occurred together in the following locations: Restingue, Cerro Culón, Río Ventana, Tembladera, Punta Blanca, Cerro Hoya National Park, Cerro Moya, Jobero, Cambutal, Altos de Güera, Río Güera, La Tronosa Forestal Reserve, El Cortezo, Quema, Guánico, Tonosí, Cacao, Cañas, Venao, Los Pozos, Macaracas, Las Palmas, Llano de Piedra, Mogollón, Cerro Canajaguas, Cerro El Vijía, Valle Rico, La Miel, Valle de Tonosí, Flores (Los Santos), Oria, Río Purio, Los Ñopos, El Cacarañal, Macaraquitas, La Llanita, Buena Vista, Mariato, Arenas, and Flores (Veraguas) (Méndez-Carvajal 2008) (Table 3).

Populations by region

Northern Region: Herrera Province (lowland). The largest howler population was found in the northern lowland region; 261 howler monkeys in 11 groups. Group size averaged 23 individuals (range 15–39); all in highly fragmented forests. Average group composition was 6.0 males (25%), 7.8 females (32%), 6.6 juveniles (27%) and 3.4 infants (14%). The adult male/female ratio was 1:1.3, female/juvenile 1:0.8, and female/infant was 1:0.4. Densities were

Table 2. Summary of survey activities from 2001 to 2009. Average survey time was 12 hrs/day. P/A: Presence/absence; ST: Strip Transects; RC: Road counts; T: Triangulation. Regions described in Table 1.

Initial date	Final date	Region	No. of observers	Days worked	Survey time (hrs)	Method applied
4/21/2001	4/25/2001	Northern (l)	6	5	360	P/A, ST, RC,T
5/21/2001	5/25/2001	Northern (l)	6	5	360	P/A, ST, RC,T
8/8/2001	8/12/2001	Northern (h)	3	5	180	P/A, ST, RC,T
12/5/2001	12/9/2001	Northern (l)	2	5	120	P/A, ST, RC,T
1/15/2002	1/25/2002	Northern (h)	9	10	1080	P/A, ST, RC,T
2/21/2002	2/25/2002	Northern (h)	2	5	120	P/A, ST, RC,T
4/21/2002	5/1/2002	Northern (h)	9	10	1080	P/A, ST, RC,T
7/11/2002	7/15/2002	Northern (h)	2	5	120	P/A, ST, RC,T
3/7/2003	3/16/2003	Northern (l) & Eastern	3	10	360	P/A, ST, RC,T
1/24/2004	1/2/2004	Eastern	7	10	840	P/A, ST, RC,T
5/1/2005	5/10/2005	Eastern	2	10	240	P/A, ST, RC,T
5/25/2006	6/3/2006	Northern (l) & Eastern	3	10	360	P/A, ST, RC,T
1/5/2007	1/15/2007	Northern (l), Eastern, Western & Southern	6	11	792	P/A, ST, RC,T
5/19/2008	5/29/2008	Northern (l) & Eastern, Western & Southern	8	10	960	P/A, ST, RC,T
4/25/2009	5/25/2009	Northern (l), Eastern, Western & Southern	7	10	840	P/A, ST, RC,T
Total			**mean = 5**	**121**	**7,812**	

Table 3. Localities confirmed with presence/absence of *A. coibensis trabeata* and *A. geoffroyi azuerensis,* Azuero Peninsula, Panama. ? = probably present; +? = high probability of presence.

	Localities	**District**	**Province**	***A.c. trabeata***	***A.g. azuerensis***
	Northern Region	**Ocú**	**Herrera**	**Absent**	**Absent**
1	Ocú	Ocú	Herrera	Absent	Absent
2	Las Animas	Ocú	Herrera	Absent	Absent
3	La Polonia	Ocú	Herrera	Absent	Absent
4	El Calabazal	Ocú	Herrera	Present	Absent
5	Camarón	Ocú	Herrera	Present	Absent
6	Tijeras	Ocú	Herrera	Present	Absent
7	Quebrada Limón	Ocú	Herrera	Present	Absent
8	Llano Grande	Ocú	Herrera	Present	Absent
9	Llano Hato	Ocú	Herrera	Present	Absent
10	Santa Mónica	Ocú	Herrera	Present	Absent
11	La Chavarría	Ocú	Herrera	Present	Absent
12	Aguas Buenas	Ocú	Herrera	Present	Absent
13	Cerro Noneca	Ocú	Herrera	Present	Absent
14	Cerro Lavadero	Ocú	Herrera	Present	Absent
15	Cerro Comején	Ocú	Herrera	Present	Absent
16	Los Carates	Ocú	Herrera	Present	Absent
17	El Cercado	Ocú	Herrera	Present	Absent
18	Las Manuelas	Ocú	Herrera	Present	Absent
19	Pedernal	Ocú	Herrera	Present	Absent
20	Santo Domingo	Ocú	Herrera	Present	Absent
21	Los Higos	Ocú	Herrera	Present	Absent
22	Potuguilla	Ocú	Herrera	Present	Absent
23	Los Asientos	Ocú	Herrera	Present	Absent
24	Parita	Parita	Herrera	Present	Absent
25	Cabuya	Parita	Herrera	Present	Absent
26	Candelaria	Parita	Herrera	Present	Absent
27	Portobelillo	Parita	Herrera	Present	Absent
28	Cerro Tigre	Parita	Herrera	Present	Absent
29	Queb. Grande	Parita	Herrera	Present	Absent
30	Río Parita	Parita	Herrera	Present	Absent
31	Llano La Cruz	Parita	Herrera	Present	Absent
32	Río Viejo	Parita	Herrera	Present	Absent
33	Las Gardenias	Parita	Herrera	Present	Absent
34	Los Lajones	Parita	Herrera	Present	Absent
35	Queb. Carrizal	Parita	Herrera	Present	Absent
36	Valencia	Parita	Herrera	Present	Absent
37	Chepo	Las Minas	Herrera	Present	Absent
38	El Ñuco	Las Minas	Herrera	Present	Absent
39	Sonadora	Las Minas	Herrera	Present	Absent
40	Tres Puntas	Las Minas	Herrera	Present	Absent
41	Alto del Higo	Las Minas	Herrera	Present	Absent
42	R. Forestal El Montuoso	Las Minas	Herrera	Present	Absent
43	Queb. Chuérala	Las Minas	Herrera	Present	Absent
44	Caras Pintadas	Las Minas	Herrera	Present	Absent
45	Río La Villa	Las Minas	Herrera	Present	Absent
46	Río Tebario	Las Minas	Herrera	Present	Absent
47	Los Pozos	Las Minas	Herrera	?	Absent
48	La Arena	Las Minas	Herrera	?	Absent
49	El Calabacito	Macaracas	Herrera	?	Absent
50	La Mesa	Macaracas	Herrera	?	Absent
	Western Region				
51	Ponuga	Mariato	Veraguas	Present	Absent
52	Tebario	Mariato	Veraguas	Present	Absent
53	Llano de Catival	Mariato	Veraguas	Present	Absent
54	Malena	Mariato	Veraguas	Present	Absent
55	La Loma	Mariato	Veraguas	Present	?

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Table 3. *continued from previous page*

	Localities	**District**	**Province**	***A.c. trabeata***	***A.g. azuerensis***
56	Río Varadero	Mariato	Veraguas	Present	?
57	Cerro La Honda	Mariato	Veraguas	Present	+?
58	Río Quebro	Mariato	Veraguas	Present	Present
59	Arenas	Mariato	Veraguas	Present	Present
60	Restingue	Mariato	Veraguas	Present	Present
61	Río Pavo	Mariato	Veraguas	Present	Absent
62	Q. MIDA	Mariato	Veraguas	Present	Absent
63	Playa Malena	Mariato	Veraguas	Present	Absent
64	Torio Arriba	Mariato	Veraguas	Present	Present
65	Changüales	Mariato	Veraguas	Present	+?
66	La Burra	Mariato	Veraguas	Present	+?
67	El Cortezo	Mariato	Veraguas	Present	+?
68	Playa Mariato	Mariato	Veaguas	Present	+?
69	Cerro Culón	Mariato	Veraguas	Present	Present
70	Río Ventana	Mariato	Veraguas	Present	Present
	Southern Region				
71	Tembladera	Mariato	Veraguas	Present	Present
72	Punta Blanca	Mariato	Veraguas	Present	Present
73	Parque Nacional Cerro Hoya	Mariato	Veraguas	Present	Present
74	Jobero	Tonosí	Los Santos	Present	Present
75	Cambutal	Tonosí	Los Santos	Present	Present
76	Altos de Güera	Tonosí	Los Santos	Present	Present
77	Río Güera	Tonosí	Los Santos	Present	Present
78	Reserva Forestal La Tronosa	Tonosí	Los Santos	Present	Present
79	El Cortezo	Tonosí	Los Santos	Present	Present
80	Quema	Tonosí	Los Santos	Present	Present
81	Guánico	Tonosí	Los Santos	Present	Present
82	Tonosí	Tonosí	Los Santos	Present	Present
83	Río Agua Buena	Tonosí	Los Santos	Present	+?
84	Río Ojo de Agua	Tonosí	Los Santos	Present	+?
85	Río Cigüa	Tonosí	Los Santos	Present	+?
86	Río de Cañas	Tonosi	Los Santos	Present	+?
87	Cacao	Tonosí	Los Santos	Present	Absent
88	Loma La Zahina	Tonosí	Los Santos	Present	Present
89	Cañas	Tonosí	Los Santos	Present	Present
90	Venao	Pedasí	Los Santos	Present	Present
91	Los Pozos	Tonosí	Los Santos	Present	Absent
92	Macaracas	Tonosí	Los Santos	Present	?
93	Las Palmas	Tonosí	Los Santos	Present	?
94	Llano de Piedra	Tonosí	Los Santos	Present	?
95	Mogollón	Tonosí	Los Santos	Present	?
96	Cerro Canajaguas	Tonosí	Los Santos	Present	?
97	Cerro El Vijía	Tonosí	Los Santos	Present	Present
	Eastern Region				
98	Valle Rico	Las Tablas	Los Santos	Present	Present
99	La Miel	Las Tablas	Los Santos	Present	Present
100	Oria	Las Tablas	Los Santos	Present	Present
101	Oria Abajo	Las Tablas	Los Santos	Present	Present
102	Queb. Pixbae	Las Tablas	Los Santos	Present	Present
103	Queb. La Palma	Las Tablas	Los Santos	Present	Present
104	Río Purio	Las Tablas	Los Santos	Present	Present
105	Queb. Nuario	Las Tablas	Los Santos	Present	Present
106	Finca Domínguez	Las Tablas	Los Santos	Present	Present
107	Finca Pillo González	Las Tablas	Los Santos	Present	Present
108	Los Ñopos	Las Tablas	Los Santos	Present	Present
109	El Cacarañal	Las Tablas	Los Santos	Present	Present
110	Macaraquitas	Las Tablas	Los Santos	Present	Present

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Table 3. *continued from previous page*

	Localities	**District**	**Province**	***A.c. trabeata***	***A.g. azuerensis***
111	Cerro Quema	Las Tablas	Los Santos	Present	Present
112	La Llanita	Las Tablas	Los Santos	Present	Present
113	Buena Vista	Las Tablas	Los Santos	Present	Present
114	Punta Blanca	Las Tablas	Los Santos	Present	Present
115	El Sesteadero	Pocrí	Los Santos	?	Absent
116	Río Mensabé	Pocrí	Los Santos	?	Absent
117	La Palma	Pocrí	Los Santos	Present	Present
118	Quebrada El Hato	Pocrí	Los Santos	?	?
119	Rio Pocrí	Pocrí	Los Santos	?	?

Table 4. Total individuals detected of *Alouatta coibensis trabeata*, Azuero Peninsula, Panama. Confidence Level (95%), mean = 9.6 individuals/groups (3–26) (SD ±3.3).

Region	**Total**	**Total groups**	**Density ind/km²**	**Density groups/km²**	**SD±**	**Area (km²)**	**Vegetation**
Northern (lowland)	261	11	40.4	1.7	9.4	6.46	Patches and living fences
Northern (highland)	37	6	0.5	0.08	3.6	69.83	Secondary forest
Southern	35	11	5.1	1.17	5.5	6.78	Secondary forest
Eastern	76	12	42.6	5.5	2.8	1.82	Gallery forest
Western	43	5	17.2	2	5.5	2.50	Gallery forest
Total	**452**	**45**	**5.2**	**0.5**	**4.8**	**87.39**	

Table 5. Total individuals detected of *Ateles geoffroyi azuerensis*, Azuero Peninsula, Panama. Confidence Level (95%) mean = 10.2 individuals/groups (4-22) (SD ±1.5) *See Table 1, **Calculated by locals and environmental authorities.

Region	**Total**	**Total groups**	**Density ind./km²**	**Density groups/km²**	**SD±**	**Area (km²)**	**Vegetation**
Northern (lowland)	_	_	_	_	_	6.46	Patches and living fences
Northern (highland)	_	_	_	_	_	69.83	Secondary forest
Southern	49	4	7	0.6	1.5	6.78	Secondary forest
Eastern	25	1	13.7	0.5	1.5	1.82	Gallery forest
Western	50**	_	20	_	_	2.50	Gallery forest
Total	**124**	**5**	**1.4**	**8.4**	**1.5**	**87.39**	**Various***

40.4 individuals/km², and 1.7 groups/km² (n = 5; SD ±9.4) for 6.46 km² forest surveyed. This population is not heavily hunted and has no natural predators, and the howlers appear to be overcrowded in the small fragments where they remain, facing, as they do, the difficulties of dispersing over wide expanses of pasture. Azuero spider monkeys were not found in this area.

Northern Region: Herrera Province (highland). The howler population was estimated at 37 individuals in six groups, with an average of 6.1 individuals per group (range 5–12). The six groups averaged 1.83 males (30%), 2.5 females (40%), 1.0 juvenile (16.4%), and 0.8 infants (13.6%). The ratio of adult male/female was 1:1.36, female/juvenile was 1:0.4, and female/infant was 1:0.3. Densities were estimated at 0.52 individuals/km² and 0.08 groups/km² (n = 6, SD ±3.6) over an area of 69.83 km² (Table 4). Azuero spider monkeys were not found in this region but interviews assured us of their presence in the past. Locals told us that Azuero spider monkeys were present in the El Montuoso Forest Reserve about 20 years ago, but disappeared later with other animals such as jaguars; eliminated by poachers (Table 5).

Southern Region: Veraguas and Los Santos provinces – howler monkey population. The howler population was estimated to be at least 35 individuals in 11 groups, with an average of four individuals per group (range 1–12; n = 7), with 1.6 males (45%), 1.6 females (45%), 0.7 juveniles (2%) and 0.4 infants (1%). Relative densities were 5.1 individuals/km² and 1.17 groups/km² (SD ±5.5 for 6.78 km²). The ratio of adult males to females was 1:1, juveniles/females was 1:0.46, and females/infants 1:0.23. Densities were calculated based on the size of each patch of forest sampled, with 3.4 individuals/km² and 0.94 groups/km² for the area in the southwest (5.28 km²), and 13.3 individuals/km² and 2.6 groups/km² for the population in the southeast (1.5 km²).

Southern Region: Veraguas and Los Santos provinces – spider monkey population. Anecdotal reports from the communities of Ventana and Tembladera (Veraguas) indicated that spider monkeys occasionally traverse the area through the gallery forest and forest fragments close to the coast. They reported that spider monkeys inhabit mostly the upper forested slopes of the mountains, and are scarce in the lowlands. People from Ventana and Tembladera (Veraguas) told us that Azuero spider monkeys normally come down near to human settlements during the rainy season (middle of May to December). For Los Santos province, we found a total of 49 spider monkeys in four isolated groups (mean size = 10.2; range 4–22). The group composition average was 2 males (SD ±1.6; 40%), 2.2 females (SD ±1.5; 44%), 1.8 juveniles (SD ±1.5; 36%) and 1.5 infants (SD ±1.5; 30%) at Venao, La Zahina, Cañas, Flores of Tonosi and Pedasi District (Los Santos). The ratio of adult males to females was 1:1, and the female/infant ratio was 1:1.5 (n = 4; 95% confidence). Densities calculated were 7.3 individuals/km^2 and 0.6 groups/km^2 in 6.78 km^2 (Table 5).

Eastern Region: Los Santos Province – howler monkey. Seventy-six howler monkeys were found in an area of 1.82 km^2. There were 12 groups, and a lone juvenile female. The group composition averaged 1.6 males (21%), 3.8 females (50%), 0.6 juveniles (7.8%) and 1.6 infants (21%), and group size averaged 7.6 individuals (SD ±2.8, n = 10, range 3–12). The ratio of males/females was 1:2.3, juveniles/females 1:2.6, and infants/females with 1:0.42. Relative densities for the Eastern Region for Azuero howler monkeys were 42.6 individuals/km^2 and 5.5 groups/km^2.

Eastern Region: Los Santos Province – spider monkeys. We found one group composed of three subgroups of Azuero spider monkeys in this region with 25 individuals seen, in the area of La Miel, Las Tablas, and the Tonosi Valley, about 2 km from the town of Flores. Average group size was 12, and subgroup size 6.2, sharing the same area with Azuero howler monkey groups. The density in the three locations was 13.7 individuals/km^2, 0.5 groups/km^2, and 2.2 subgroups/km^2, respectively. Subgroup composition averaged 2.0 adult males, 2.3 adult females, 1.3 juveniles, 1.3 infants (range 3–14, SD ±1.5, n = 3) for a total area of 1.82 km^2. These monkeys are indirectly connected between the Río Oria Arriba and Oria Abajo via the La Palma Bridge as far as the forest of Cerro El Montuoso, Las Tablas District.

*Western Region: Southern Veraguas Provinc*e. We observed 43 Azuero howler monkeys in five groups. The groups averaged 1.5 males (13.9%), 5.2 females (48.8%), 3 juveniles (13.9%) and 2.5 infants (23.2%). The adult male/female ratio was 1:3.5, female/juvenile 1:0.4, and females/infant 1:0.5. Densities calculated were 17.2 individuals/km^2 and 2 groups/km^2 (n = 4; SD ±5.5) in 2.5 km^2. Spider monkeys were reported by the locals, and around 50 individuals were confirmed for Cerro Hoya National Park, Arenas, Quebro and Restingue including Cerro Culón (Table 5).

Total population of the Azuero howler monkey

We recorded 433 Azuero howler monkeys from 87.39 km^2 of fragmented forest from 2001 through 2009 (Table 4). Forty-three groups provided an overall density of 5 individuals/km^2 and 0.5 groups/km^2 for the entire forested area of the Azuero Peninsula (n = 32, SD ±2.4). Overall, group composition averaged 2.5 adult males, 4.3 adult females, 1.92 juveniles and 1.88 infants. The mean group size was 9.6 (range 3–26). According to the equation, Ň = 433/(1)0.14, we estimate a total of 3,092 individuals remaining in the wild.

Total population of the Azuero spider monkey

We recorded 74 Azuero spider monkeys, with five groups detected and/or counted directly, and six indirectly (Table 5). There are evidently no spider monkeys remaining in Herrera province, the northern part of the Azuero Peninsula, but remnant and diminished populations survive in the southern (southeastern and southwestern) parts of the peninsula (Méndez-Carvajal and Ruiz-Bernard 2009). The Cerro Hoya National Park is their main stronghold (Rowe 2000; Cuarón *et al.* 2008), and our efforts were concentrated mostly in remnant forests. We found the Azuero spider monkeys surviving in the remnant patches close to the Cerro Hoya National Park and La Tronosa Forest Reserve, and we also confirmed their presence in the surrounding secondary forest, living fences and forest patches throughout the southeastern part of the peninsula, including the gallery forest and coastal forests (Fig. 1). The spider monkeys were difficult to observe in the wild, but using presence/absence detection we obtained a total of 13 localities where their presence was confirmed; in seven of them we obtained direct counts. Conservatively, we can assume at least one subgroup is present in each of the other six (widely separated and isolated) areas. Adding 50 to the number of individuals recorded in the southeastern gallery forested areas (74 individuals), 124 individuals was the number detected during our surveys. Applying the formula β = 124/(1)0.85, I estimate a total of 145 Azuero spider monkeys remaining in the wild.

Discussion

Distribution

Cattle pasture and farmland dominate the landscape of the Azuero Peninsula, largely replacing the original forest (Heckadon-Moreno 2001). The most heavily disturbed parts are in central and northern Azuero, with urbanization more widespread and large areas of monoculture crops, besides cattle ranching (Suárez 1981). Despite this, *Alouatta c. trabeata*, generally scarce by any standards, was found to be widespread and occupied several different habitat types, from sea level to 1500 m. My results show evidence of a significant presence of Azuero howler monkeys and spider monkeys in forest patches with such as *Anacardium excelsum, Bursera simaruba*, *Cecropia* spp., *Ceiba pentandra*, *Enterolobium cyclocarpum*, *Ficus* spp., *Manguifera indica*, *Inga vera*, *Pachira* spp., and *Spondias mombin* (see Table 6); species that are generally conserved by the Azuerense campesinos as living fences on their cattle ranches (Méndez-Carvajal 2008). Previous reports of *A. c. trabeata* and *A. g. azuerensis* (Brandaris 1983; Rowe 2000) also found them surviving in extensively deforested areas of cattle ranches and gallery forest.

Alouatta c. trabeata is not restricted to the Cerro Hoya National Park. It would seem, on the other hand, that *A. g. azuerensis*, no longer occurs in El Montuoso Forest Reserve (EMFR), thought to be an important protected area for this species by Cuarón *et al*. (2008). The Azuero howler monkey is common in riparian forest and is often sighted moving through gallery forest, living fences and patches of forest of the natural reserves of Azuero (Méndez-Carvajal *et al.* 2004; Méndez-Carvajal 2005; Méndez-Carvajal and Ruiz-Bernard 2009). The Azuero spider monkey has been extirpated from the El Montuoso Forest Reserve (EMFR) and non-protected areas in Herrera province; it is now found only in the southern part of the peninsula, including the Mariato District (Veraguas province), Cerro Hoya National Park and La Tronosa Forest Reserve (Los Santos province) (Méndez-Carvajal and Ruiz-Bernard 2009). Deforestation and hunting has severely reduced and fragmented the ranges of *A. c. trabeata* and *A. g. azuerensis* in the region, mainly by eliminating suitable habitat, most particularly along the middle and northern parts of Azuero.

Table 6. Common trees species identified for the study areas surveyed and observed to be used by Azuero primates, Azuero Peninsula, Panama. A) Northern Region (l); B) Northern Region (h); C) Southern Region; D) Eastern Region; E) Western Region. Species of trees confirmed, according to Pérez and Deago (2001), Garibaldi *et al*. (2004), and Agustin Somoza in Méndez-Carvajal (2005).

Tree Species	**Common name**	**A**	**B**	**C**	**D**	**E**
Amaioua corymbosa	Madroño		×			
Anacardium excelsum	Espavé	×		×		×
Apeiba tiborbou	Cortezo		×			
Astronium graveolens	Zorro				×	
Brosimum guianense	Verbá		×			
Bursera simaruba	Carate	×	×	×	×	×
Cassipourea elliptica	Bocaculebra		×			
Cedrela odorata	Cedro amargo				×	
Ceiba pentandra	Ceiba			×		×
Cordia alliodora	Laurel				×	
Dalbergia retusa	Cocobolo				×	
Diphysa robinoides	Macano	×				
Enterolobium cyclocarpum	Corotú	×		×		×
Ficus crocata	Higuerón		×			
Ficus yoponensis	Higuerón	×		×		×
Garcinia intermedia	Madroño	×				
Guazuma ulmifolia	Guácimo	×		×		×
Gustavia superba	Membrillo	×				
Inga vera	Guaba	×		×		×
Jacaranda copaia	Jacaranda	×		×		×
Miconia donaeana	Palo de seno		×			
Myrciaria floribunda	Guayabillo		×			
Ocotea dendrodefne	Sigüa	×				
Pachira quinata	Cedro Espino			×	×	×
Pachira spp.	Yuco de monte			×		×
Platymiscium pinnatum	Quira				×	
Quercus lancifolia	Monterillo		×			
Roupala montana	Carne asada		×			
Simarouba amara	Aceituno		×			
Spondias mombin	Jobo	×		×		×
Tabebuia guayacan	Guayacán amarillo					
Tabebuia rosea	Roble				×	
Ternstroemia tepezapote	Manglillo		×			
Virola sebifera	Fruta dorada		×			
Vochysia ferruginea	Mayo		×			
Xylopia spp.	Malagueto	×				
Zanthoxylum panamense	Tachuelo		×			

The extirpation of *A. g. azuerensis* from the El Montuoso Forest Reserve shows that its occurrence in a protected area is no guarantee of its survival. The Azuero spider monkey was hunted out by indigenous people and farmers. Hunting pressure seems to be less, however, for *A. c. trabeata*, and the howler monkey is evidently more adaptable than the spider monkeys.

The forests harboring *A. c. trabeata* and the Panamanian white-throated capuchin, *Cebus capucinus imitator*, in the southwestern part of the peninsula are classified as evergreen subtropical lowland and montane forest, but in the southeast semideciduous and largely secondary forest prevail (Garibaldi *et al.* 2004; Pérez and Deago, 2001). Important for these species and for *A. g. azuerensis* in the south is the Cerro Hoya National Park, and the riparian vegetation along the Ventana town border as far as Cambutal, then following the mangroves of the southeastern coast of Azuero mixing with the gallery forest and patches of forest near the coast in the vicinity of Tonosi, Venao, Cañas as far as Pedasi (Fig. 1.).

Population estimates for the Azuero howler and Azuero spider monkey

The population estimates for the howler and spider monkeys from Azuero have changed from previous calculations made in 2008 (Méndez-Carvajal and Ruiz-Bernard 2009). The estimate for the spider monkey has increased slightly, from 117 to 145 individuals still surviving in Azuero. That for the howlers, on the other hand has dropped with an increase in the area covered by the surveys, from 4,214 in 2008 to around 3,092 (Méndez-Carvajal 2008). Not all the locations surveyed had both species; howler monkeys demonstrated better plasticity in deforested zones, as found by Clarke *et al*. (2002) and Baumgarten and Williamson (2007). *Alouatta* does better than *Ateles* in fragmented habitats.

Population densities

Densities of *A. c .trabeata* of 0.52 individuals/km² for the northern highlands and 2.2 individuals/km² for the lowlands are evidently low when compared to estimates in other areas; for example, *A. palliata* in Los Tuxtlas, Mexico, with 23 individuals/km² (Estrada and Coates-Estrada 1996); La Selva, Costa Rica, with 12.2 individuals/km² (Fishkind and Sussman 1987), and Barro Colorado Island, Panama, with 91.7 individuals/km² (Milton 1992). One possible factor in this is that *A. coibensis* has a tendency to live in smaller unimale-multifemale, groups than *A. palliata* elsewhere in Mesoamerica (Méndez-Carvajal and Serio-Silva 2011). The difference in population densities between highland and lowland areas may be related to lower nutrient availability at higher altitudes (600–1,559 m above sea level) where temperatures are lower (Chapman and Balcom 1998). Morales-Jiménez (2002) found differences in group sizes for *Alouatta seniculus* in the Andes, with 3.1 individuals/group in high elevations, and 6.9 individuals/group in the lowlands, similar to our groups. Our survey found no effect of elevation on population density (Spearman rank correlation coefficient 0.045, n=31, p=0.811). For highlands in Azuero (600 m), lower densities of howlers could be caused by hunting; for food in the Sonadora area behind the EMFR (northern region, highland), and also in the Cerro Hoya National Park for traditional medicinal potions, influenced directly by the Ngäbe Buglé indigenous people (Torres de Araúz 1980).

In the eastern region, the densities of *A. c. trabeata* were 42.6 individuals/km², but much lower on the western side of Azuero at 17.2 individuals/km². This could be explained by the connectivity of living fences, widespread on the western side; allowing the monkeys to move more easily through the landscape. Even if howler monkeys adapt well to surviving in disturbed forests (Ferrari 2002), overcrowding with the lack of migration is a problem. The local people on the east side of the Azuero Peninsula are more tolerant and protective of howler monkeys and exploit the forest fragments less for such as charcoal and medicinal products.

Azuero spider monkeys with 1.4 individuals/km² for fragmented habitat suffer more from hunting pressure and the use of the forest patches by people (Méndez-Carvajal and Ruiz-Bernard 2009). Densities in this study were similar to those in other areas where they are hunted; for example, Boca de Cupe, Darien, Panama, with 3.6 individuals/km²; (Moreno-Ruíz 2006), and lower than those recorded from Tikal, Guatemala (*A. g. yucatanensis*) with 24 individuals/km² (Cant 1990). Densities of *A. g. frontatus* have been estimated at 9 individuals/km² in the Santa Rosa Natural Park, in Costa Rica (Freese 1976). Except for the Río Oria and La Miel area, the Azuero spider monkey has been found only as family groups (male, female, juvenile and infants), contrasting with a typical spider monkey sub-grouping system (Carpenter 1935; Aureli and Schaffner 2008).

Group composition: Azuero howler monkey

The Azuero howlers in the lowlands tended to have larger groups. The howlers from the Northern (lowland) community had an average of 23.8 individuals/group (15–39) (Méndez-Carvajal 2005), which is high when compared with the average of the Azuero howler populations elsewhere with 6.1–10.0 individuals/group (3–12) (Méndez-Carvajal *et al.* 2004). Due to the abundance of trees reported as potential resources for howlers in the Azuero area, we could expect them to be more abundant with larger groups in the Northern region (lowland), as was found on Barro Colorado Island (BCI) Panama. Statistical analysis of Azuero howler group structure vs. habitat size was applied in this study using Spearman's test, showing a positive correlation (-4.50, n=31, p=0.011), confirming the hypothesis that groups in the eastern region are a slightly more connected through small patches (linear shape home-ranges), while the Northern region groups are more isolated (Fig. 1).

Group structure presented differences in the male/female ratio, and was found to be more uni-male than multi-male, contrary to the first report of the Azuero howler monkeys in the Northern region (lowland) (Méndez-Carvajal 2005). The group composition was similar to that found for *A. c. coibensis* on Coiba Island, with 1.8 for males and 2.8 for females (Milton and Mittermeier 1977; Méndez-Carvajal *et al.* 2010b).

Group composition: Azuero spider monkey

The subgroup size average of the Azuero spider monkey, 3.8 individuals/subgroup, is comparable with that found for *A. fusciceps rufiventris* at 4 individuals/subgroup (Méndez-Carvajal *et al.* (2010a), and 3.5 individuals/subgroup for Venezuelan *A. hybridus* (see Cordero-Rodríguez and Biord 2001). *Ateles g. azuerensis* was found in smaller groups (12 individuals/group) in forest patches in the southern area; La Miel, Flores, Oria and Cañas. Total size of groups of Azuero spider monkeys could be considered low in devastated areas if we compare them with averages found in protected areas such as Calakmul Reserve or Quintana Roo, Mexico (28.5 individuals/group) (Ramos-Fernández *et al.* 2003; Estrada *et al.* 2004), Barro Colorado, Panama (24 individuals/group) (Di Fiore and Campbell 2007) and *Ateles fusciceps rufiventris* from Chucanti-Darien, Panama, with average of 30 individuals/group (Méndez-Carvajal *et al.* 2010a).

Conservation Status

Deforestation has been the principal threat to these subspecies. Land use in Azuero is agricultural. If the region is well supported economically, based on small, medium or large businesses, subsistence hunting could be minimal. Previous questionnaires given out before the start of this project in 2001 found that monkeys are not a vital resource for Azuero locals (Ruiz-Bernard *et al.* 2010). Environmental education and awareness programs informing the communities of the value of their forests and living fences, and of the ecological role of the primates, could be highly positive for the conservation of the region's primates. It will be important to set up a permanent monitoring program for the two primates and their habitats.

Our informal interviews with the people from the communities revealed two issues of relevance: (1) the lack of any informative material that values the region's fauna and flora, and (2) the lack of interest in protecting wildlife, especially these monkeys which are considered to be little more than crop pests. The Fundación Pro-Conservación de los Primates Panameños (FCPP) has been offering educational talks to elementary schools and colleges to create a basic conservation understanding for the future generations of the Azuero people (Ruiz-Bernard *et al.* 2010). FCPP is still monitoring the groups found in the natural reserves of Azuero.

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GIS Risk Assessment and GAP Analysis for the Andean Titi Monkey (*Callicebus oenanthe*)

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Abstract: We conducted a predictive GIS (Geographical Information System) analysis to create a realistic Habitat Suitability Model (HSM) and risk analysis throughout the distribution of the Andean titi monkey (*Callicebus oenanthe*) in order to evaluate the effectiveness of the current protected area (PA) network. This was done to help current conservation work and aid in the planning and implementation of future initiatives. Little was known about this species until recently. *Callicebus oenanthe* is listed as Critically Endangered on the *IUCN Red List of Threatened Species.* It is endemic to San Martín region, northeastern Peru. Our results show that the extent of habitat available for this species may be greater than previously thought but that habitat loss in the region is extremely high. GAP analysis indicates that the current protected area network is ineffective in protecting this species, and new reserve areas are urgently needed. We recommend further study into the species' ecology to better understand its needs and to aid in future conservation work.

Key Words: Andean titi monkey, *Callicebus oenanthe,* GIS, deforestation, conservation

Introduction

The Andean titi monkey (*Callicebus oenanthe*) is one of Peru's three endemic primates, together with the yellow-tailed woolly monkey (*Oreonax flavicauda*) and the Peruvian night monkey (*Aotus miconax*). *Callicebus oenanthe* is only found in the San Martín region of northeastern Peru (DeLuycker 2006; Bóveda-Penalba *et al*. 2009). This species is listed on Appendix II of CITES (2011), as Critically Endangered (Categories A2cd) on the IUCN *Red List of Threatened Species* (Veiga *et al*. 2011) and as Vulnerable under Peruvian Law (Decreto Supremo Nº 034-2004-AG). Until recently, very little investigation has been conducted on this species in the wild (Mark 2003; Rowe and Martinez 2003; DeLuycker 2006; Aldrich *et al*. 2008; Bóveda-Penalba *et al.* 2009).

Until 2003, *Callicebus oenanthe* was only known from a handful of sightings and some few museum collections (Bóveda-Penalba *et al.* 2009). Since then further short ecological studies have been conducted (Mark 2003; DeLuycker 2006; Aldrich *et al*. 2008). In 2007, the first long-term survey of this species began (Bóveda-Penalba *et al.* 2009) to determine its actual distribution and conservation status. *Callicebus oenanthe* has an extremely limited geographic range in the Mayo and lower Huallaga river valleys (Bóveda-Penalba *et al.* 2009), part of the Tropical Andes Biodiversity Hotspot (Myers *et al.* 2000). Its preferred habitat is forests below 1,200 m above sea level in northern San Martín (Tello-Alvarado pers. obs.). Previous reports suggested that the species was restricted to the lower elevations of the Alto Mayo valley (DeLuyker 2006), particularly in gallery forests along river margins (Mark 2003). Subsequent study has confirmed the presence of this species in a greater range of habitat types, including palm-dominated forests, hilly areas, and dry forests. Bóveda-Penalba *et al*. (2009) reported that the species was present in seasonally flooded forest, but subsequent investigation shows that this is not true (unpubl. data). This is probably because of competition with *Cebus apella* and *Saimiri sciureus*.

Callicebus oenanthe has been found to be sympatric with *C. discolor* at the lower reaches of the Mayo river valley (Vermeer *et al.* 2011). Small populations of *C. oenanthe* have also been recorded on the eastern bank of the Río Huallaga (Bóveda-Penalba *et al*. 2009). Morphological differences have been reported for *C. oenanthe* populations on either side of the Río Mayo (Mark 2003; Aldrich 2006, DeLuycker 2006) and between populations in the north and south of San Martín

(Bóveda-Penalba *et al*. 2009). Most *C. oenanthe* have a white mask but differences were found in some groups in the southern end of the species' distribution which have darker coloration on the body and lack the white mask (unpubl. data). These differences appear to be purely morphological as groups of mixed types have been observed as well as a pair of white morphs with dark offspring (unpubl. data).

Callicebus oenanthe is threatened by the widespread loss of its habitat over the last three decades. Deforestation rates in northern San Martín are among the highest in the country (Peru, INEI 2008). Deforestation is fuelled by the need for agricultural land, particularly for rice cultivation, in the plains of the Mayo and middle Huallaga river valleys, and cacao on the lower slopes of the Andean cordillera (DeLuycker 2006). Legal and illegal logging also play a major role. The habitat fragmentation resulting from deforestation is another serious threat to this species (Bóveda-Penalba *et al.* 2009). The original extent of the species' habitat has been estimated at 12,000 km² (Hershkovitz 1949–1988 cited in Ayres and Clutton-Brock 1992). Forest loss in San Martín has been estimated to be at least 40% (Veiga *et al.* 2008), with most of this occurring in the low altitude river valleys. Illegal hunting for the local and national pet trade is an additional threat. We have recorded 16 individuals in illegal captivity since 2007 (unpubl. data).

Although permanent human settlements have existed in this area since colonial times, it wasn't until the 1950s that *C. oenanthe* habitat was severely threatened. Mass immigration began with the construction, and subsequent paving, of the main highway, the *Carretera Marginal de la Selva*, connecting the Peruvian coast with the Amazonian lowlands to the east. The opening of the highway led to massive immigration from the high mountain sierra of Cajamarca and coastal regions such as Piura (Peru, INEI 2011). This immigration continued with the promotion of government-sponsored settlement and agrarian reform (Rengifo-Ruiz 1994). The population of San Martín rose by 131% between 1981 and 1993 (Peru, INEI 2011). This increase is accelerating and has since risen a further 300% between 1993 and 2007 (Peru, INEI 2011).

The fact that *Callicebus oenanthe* is restricted in its altitudinal range and habitat type increases its intrinsic risk of extinction (Purvis *et al.* 2000). This, coupled with anthropogenic pressures, makes the species a priority for conservation. GIS modeling has been used in many studies to determine species distributions and gaps in protected area networks (Aspinall 1993; Mariano *et al.* 2006; Buckingham and Shanee 2009). Here we create the first realistic Habitat Suitability Model (HSM) for the Andean titi monkey, following methods used by Buckingham and Shanee (2009) to assess the yellow-tailed woolly monkey (*Oreonax flavicauda*). We used inductive GIS modeling methodology to predict the original and current extent of habitat for this species as well as to determine 'hotspots' for potential threats. We also carried out a GAP analysis of the current protected area (PA) system in San Martín to assess the extent to which *C. oenanthe* habitat is represented in PAs and to identify optimum areas for the creation of new areas and protected corridors to ensure genetic flow between populations in the future.

Methods

Callicebus oenanthe is endemic to the northern San Martín region of northeastern Peru. It is known to occur in the Mayo river valley and the western side of the middle Huallaga river valley between 5º39' and 7°06'S. The Andean titi monkey has been observed in diverse ecosystems from humid lowland rainforest to dry scrub forest (unpubl. data). It inhabits forests at altitudes of below 1,200 m above sea level. Its range is restricted by rising elevations to the north, northeast and west, partly by the Río Huallaga to the east and the Río Huayabamba to the south.

San Martín has an estimated human population of about 730,000; the most densely populated provinces are in the north of the region (Peru, INEI 2011). The species occurs in the Área de Conservación Municipal Juanjuicillo, Área de Conservación Municipal Paz y Esperanza, Área de Conservación Municipal Almendra and the Área de Conservación Municipal Mishquiyacu-Rumiyacu (Fig. 4). There are also several other small municipal conservation areas in the Alto Mayo Valley. It has also been found in areas bordering the Bosque de Protección Alto Mayo and the Área de Conservación Regional Cordillera Escalera, but its presence in these areas has not been confirmed.

Data collection

Data used in this study include point localities and other field observations, ecological niche data, land use maps and the Digital Elevation Model (DEM90 from the Shuttle Radar Topography Mission) of Peru (<http://www.srtm.usgs.gov>). We used point locality data from previous distribution surveys (Bóveda-Penalba *et al.* 2009) and data collected for this study (unpubl.).

We used ArcGIS 9.3 (ESRI 2008) for analysis and modeling. Land use maps were obtained from the Instituto de Investigación de la Amazonia Peruana (IIAP) (Peru, IIAP 2007, 2008). Distributional limits for the species were set as elevations above 1,200 m above sea alevel to the north and west, the Río Huallaga to the east and the Río Huayabamba to the south and southeast (Fig. 1). All data layers were clipped to the study area. DEM90 in raster format was reclassified to a set of 20 altitudinal classes from 0 to >2,500 m above sea level. Many of the localities for this species are from small forest patches and gallery forests not recognized on the land use maps and were not easily definable in satellite images of the study area. Forest patches and gallery forests were not included in the analysis as they probably do not constitute large areas of remaining habitat and do not provide good GAP areas for reserves. Elevation, river boundaries and vegetation types were combined to produce a map of predicted remaining habitat.

Distribution and Habitat Suitability Modeling (HSM)

Locality data were converted into decimal degrees and assigned the WGS 84 coordinate system. A kernel density transformation was applied to *C. oenanthe* point data, following Buckingham and Shanee (2009). This was used to determine 'hotspots' with higher densities of *C. oenanthe* sightings. Vegetation types used in habitat suitability modeling were those where *C. oenanthe* presence has been confirmed from field studies. These were *terrazas, bosques subandino, sabanas*, palm-dominated forests, *Ficus*-dominated forests and mixed-association (Peru, IIAP 2007). All habitat types were equally weighted for analysis. Elevation was then divided into two weighted categories: elevations of <700 m were given a 'good' rating; elevations of >700 and <1200 m were given a 'marginal' rating. Areas outside of these elevations were given a null rating. Similarly, land use types outside of the six forest types selected were given a null rating. This was used to create a map of potential remaining habitat of 'marginal' and 'good' rating (Fig. 2).

Ecological Risk Assessment and GAP analysis

ArcGIS 9.3 (ESRI 2008) was used to evaluate levels of threat to areas of suitable habitat highlighted by the HSM. Threats were determined as proximity away from human development (Peyton *et al.* 1998). Urban areas, population centers and road networks were classified as human developments. Areas highlighted by the HSM were classified to one of three threat levels based on proximity to human development (>8 km Low Risk, >3 km and <8 km Medium Risk, <3 km High Risk). A data layer showing mining concessions from the Instituto Geológico Minero y Metalúrgico (Peru, INGEMMET 2011) was then overlaid on the risk assessment layer and areas of mining concessions were removed from the layer. The final risk assessment was overlaid on the HSM layer, and areas of unsuitable habitat and high risk were removed. This was used to create a layer of 'marginal' and 'good' habitat with 'low risk' (Fig. 3).

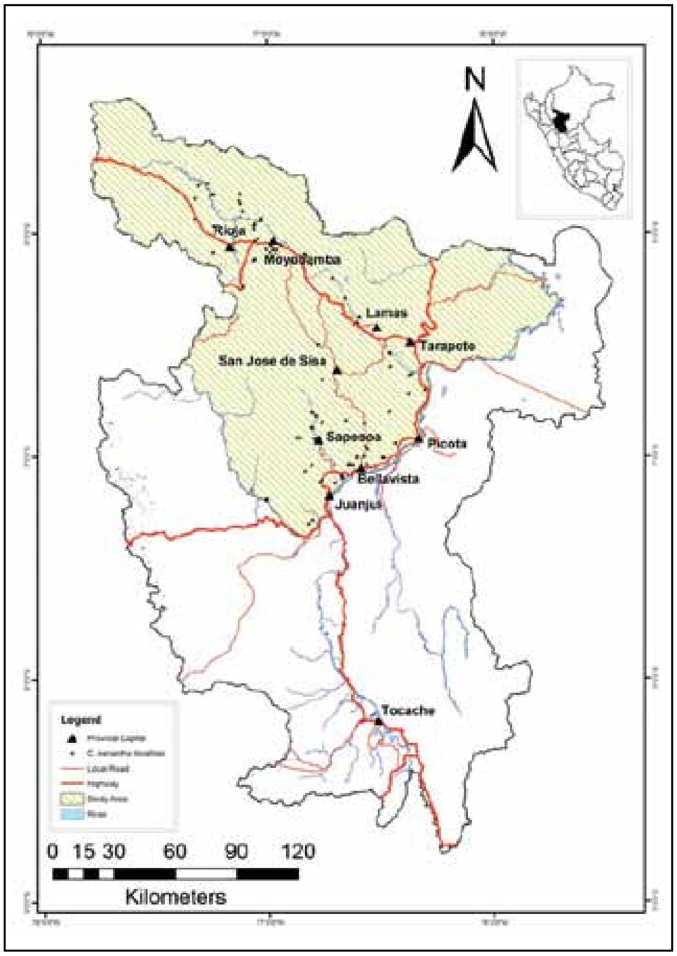

Figure 1. San Martín region. Highlighted are *Callicebus oenanthe* localities and the study area.

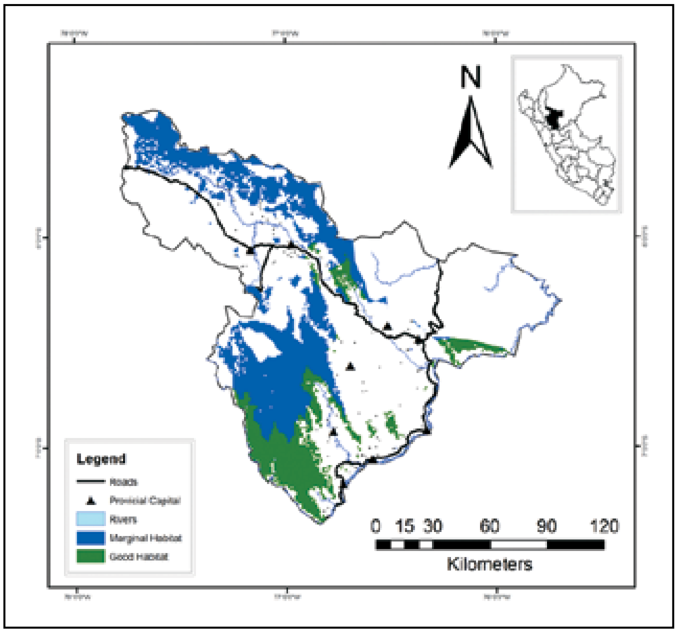

Figure 2. Estimated potential remaining habitat for *Callicebus oenanthe.*

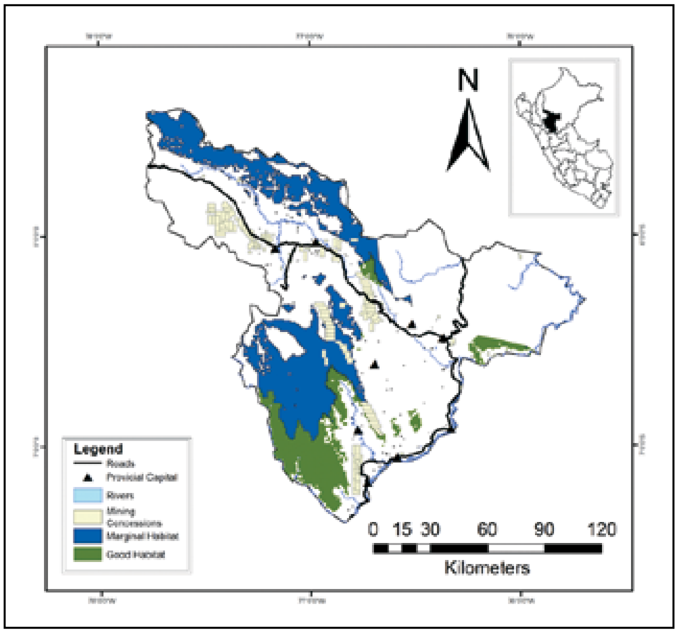

Figure 3. Estimated low risk habitat remaining for *Callicebus oenanthe*, showing mining concessions.

A PA network layer was overlaid on the HSM and risk analysis layers to highlight areas in need of attention (Fig. 4). Approximate area values were calculated for each suitability category (i.e., marginal and good). This was used to find the area of each suitability class within the existing PA network. A further data layer showing forestry concessions was overlaid on the HSM and risk analysis layers to highlight areas available for protection (Fig. 5). Forestry concessions were not considered high risk as they leave forest cover intact, removing only selected timber species. Finally, a map was generated showing habitat of 'marginal' and 'good' rating with 'no risk' which is available for protection (Fig. 6).

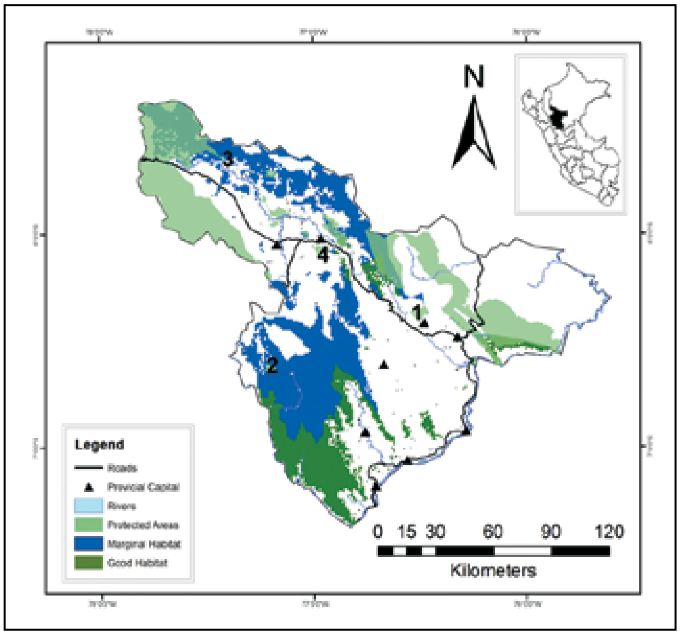

Figure 4. Low risk *Callicebus oenanthe* habitat, showing the existing protected area network. (1: Área de Conservación Municipal Juanjuicillo, 3646.1 ha, 2*:* Área de Conservación Municipal Paz y Esperanza, 1678 ha, 3: Área de Conservación Municipal Almendra, 212.3 ha, 4: the Área de Conservación Municipal Mishquiyacu-Rumiyacu, 856.5 ha)

Results

Habitat Suitability Modeling (HSM)

Total area and percentage of coverage was calculated for all levels of the analysis (Table 1). Based on habitat preferences and suitability modeling from field observation point localities, the estimated original range of *C. oenanthe* covered some 14,686 km². The current estimated extent of 'marginal' and 'good' habitat is only 6,515 km², a loss of 55.6%. The majority of habitat loss has been in the plains of the Mayo and Huallaga river valleys (Fig. 2). Of the remaining estimated habitat, only 1,930 km² is rated 'good'; equivalent to just 13% of the original extension (Table 1).

Risk Analysis

Of the remaining habitat for *C. oenanthe*, 5,710 km² is considered to be 'low risk' or 'no risk' habitat. Only 1,667 km² of this is rated as 'good' habitat (Table 1) with the largest portion in the south end of the species' distribution.

GAP Analysis

Only 14.6% of possible *C. oenanthe* habitat is currently covered by the protected area network, leaving 85% unprotected. Only 7.8% of the habitat rated as 'good' is within the network (Table 1). GAP analysis highlighted large areas of both 'marginal' and 'good' habitat that remain unprotected. It also revealed that much of the remaining habitat for the species is available for protection, although less of the remaining habitat rated as 'good' is available for protection.

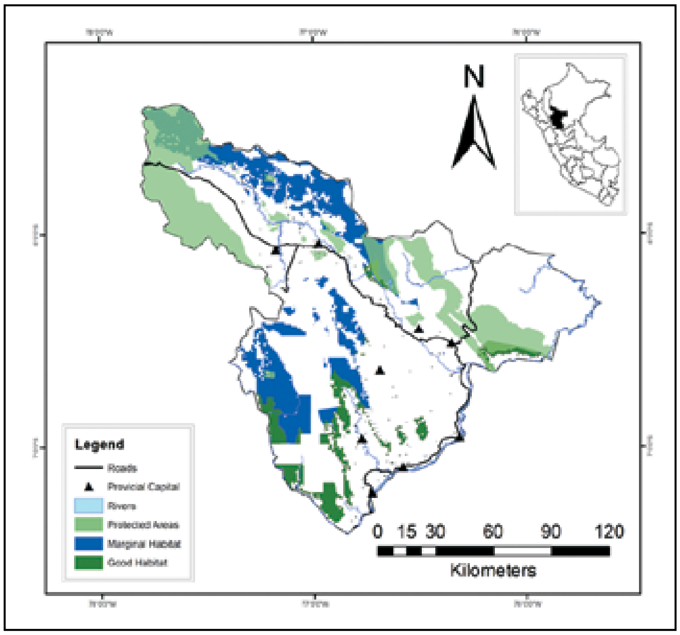

Figure 5. Areas of habitat low risk not covered by logging concessions and that therefore could be considered for protection.

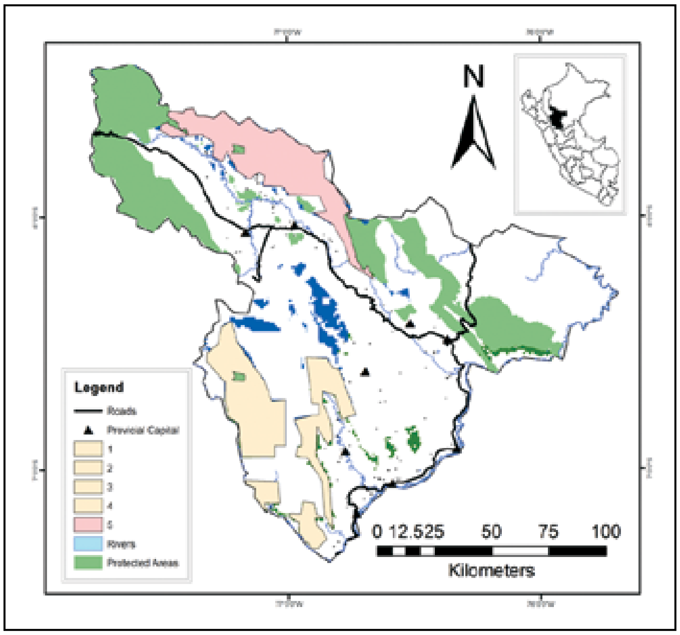

Figure 6. Existing protected areas with suggested GAP reserves and extension areas.

Four new protected areas and one wildlife corridor area are suggested based on the HSM and the results of the risk assessment (Fig. 6). Together these would protect a further 3,391 km² of remaining habitat, leaving only 2,170 km² or 33% unprotected (Table 1). Potential reserves were chosen as they covered the largest contiguous areas of good and marginal habitat available for protection. A map was created highlighting five areas for new reserves and reserve extensions to complement the existing PA network (Fig. 6).

Discussion

Previously thought to be restricted to the Alto Mayo valley (DeLuyker 2006), an area of only 6,307 km², the actual distribution of *C. oenanthe* is now known to be much larger (Bóveda-Penalba *et al.* 2009). Our calculation of the original extent of the species' distribution — 14,686 km² — is the highest estimate so far, although it is similar to a previous estimate of 12,000 km² by Hershkovitz (1949–1988), cited in Ayres and Clutton-Brock (1992). Unfortunately the parameters used for this estimate are not given.

Although records do exist of the species' presence to the east of the Río Huallaga (Bóveda-Penalba *et al.* 2009), we did not include this area in the analysis as we have the impression that these are small enclave populations that have somehow been able to pass the river (unpubl. data). Such enclave populations have also been observed for other *Callicebus* species (Hershkovitz 1988).

As with most diurnal mammals in the Neotropics, hunting and habitat loss are the main threats faced by this species (Laurance *et al.* 2000). Human population increase and associated deforestation in San Martín are amongst the highest in Peru (Peru, INEI 2011). Immigration has been facilitated by the construction of the main highway connecting this formerly remote region with the coast, furthered by the construction of rural access roads into new areas. Deforestation in the river plains of the ríos Mayo and Huallaga has left a mosaic landscape of small forest patches surrounded by agricultural land. During field surveys (Bóveda-Penalba *et al.* 2009) *C. oenanthe* was encountered in 49 forest patches ranging in size from 0.5 ha to 70 ha (average 6.43 ha ±11.9) (J. C. Tello-Alvarado unpubl. data). This not only reduces the total habitat available to *C. oenanthe* but produces several further negative effects; fragmentation increases the risk of extinction from anthropogenic pressures and independent stochastic events (Reed 2004); fragmentation reduces genetic flow between isolated populations increasing the risk of genetic degeneration through inbreeding (Lande 1998); fragmentation facilitates access for hunters (Peres 2001) and increases intra- and inter-specific competition for resources (Estrada and Coates-Estrada 1996).

Table 1. Total area habitat predictions and percentage coverage of PA network, potential habitat for protection, and suggested new reserve areas.

	All possible habitat (km²)	Marginal habitat (km²)	Good habitat (km²)
Original extension	14,686.00	8,216.44	6,469.56
Current extension	6,515.75	4,585.68	1,930.07
Low risk habitat	5,710.13	4,042.93	1,667.20
Protected habitat	953.25	802.29	150.95
Low risk protected	842.69	704.27	138.42
Not protected	5,562.50	3,783.39	1,779.12
Low risk not protected	4,867.44	3,338.66	1528.78
% Protected	14.6%	17.5%	7.8%
% Unprotected	85.4%	82.5%	92.2%
% Low risk protected	14.8%	17.4%	8.3%
% Low risk unprotected	85.4%	82.6%	91.7%
Available for protection	4,333.43	3,273.98	1,059.46
GAP reserves	3,391.34	-	-
% Protected with new reserves	66.68%	-	-

The present study was limited by the lack of detailed geographic data on forest patches in the study area. The majority of locality records for this species are within areas classed as deforested (Peru, IIAP 2007). The combined total area of patches previously surveyed (Bóveda-Penalba *et al.* 2009) was 315 ha (J. C. Tello-Alvarado unpubl. data), which represents less than 5% of the remaining habitat. Many of these patches are in areas of 'good' habitat but with a high associated risk because of their proximity to human development.

Density estimates for *C. oenanthe* range from 113 individuals/km² at Tarangue (Aldrich *et al.* 2008), a large isolated patch (about 70 ha) of mostly secondary forest, to 120 individuals/km² at Pucunucho (unpubl. data) an area of secondary forest (about 23 ha) contiguous with more extensive primary forest only through a thin corridor of forest. These density estimates are extremely high compared to other titi monkey species and could be a result of the crowding of individuals into these areas due to habitat loss in surrounding areas (inability to disperse). Such high densities in fragmented forests suggest that protection of forest fragments and connectivity between patches is of high importance for the conservation of this species.

Our study highlights the lack of protection afforded this species by the existing protected area network in San Martín, with only a very small percentage of habitat currently protected (14.6 %), and even less habitat of 'good' quality (7.8%) with low risk (14.8%). The recommendations in this study would afford the Critically Endangered *C. oenanthe* much-needed protection. Areas 1–4 (Fig. 6) could be protected at the national, regional or municipal level or protected privately as conservation concessions (*Concesión para la Conservación*), eco-tourism concessions (*Concesión para Turismo*) or private conservation areas (Área *de Conservación Privada*). Area 5 lies within native community lands and could, therefore, only be protected as a communal reserve under Peruvian law.

Urgent measures are needed to protect habitat for this species, particularly in the southern end of its distribution that still holds large areas of contiguous habitat rated as 'good' that could be given legal protection (Fig. 4). Currently two initiatives are underway to protect habitat in this area. The NGOs Neotropical Primate Conservation, *Proyecto Mono Tocón* and *Amazónicos para la Amazonia* are working together to protect three areas for the conservation of *C. oenanthe*, all of which are in the southern portion of the species' range. One private conservation area at Pucunucho currently covers about 23 ha of secondary forest but could be extended to protect a forest corridor that connects the area to a large (about 3,000 ha) area of primary habitat. Two conservation concessions are being developed in the province of Mariscal Cáceras. These areas, near the villages of Bagazán and Ricardo Palma, would cover approximately 8,000 ha of 'good' habitat.

Environmental education should be a priority throughout the species' distribution in order to highlight the threats faced and the need to preserve connectivity between patches and in gallery forests. *Proyecto Mono Tocón* has been carrying out education work since 2007, and both Neotropical Primate Conservation and *Amazónicos para la Amazonia* promote educational activities in the area focusing on habitat protection and hunting.

We recommend further investigation on the presence of *C. oenanthe* in areas highlighted by this study as 'marginal' habitat and areas in the far east of the study area and central west areas that are highlighted—previous work in these areas was unable to confirm the species presence but did encounter *C. discolor*. In addition surveys of the species densities in more areas, particularly those with more extensive forest and at different elevations, are needed to determine the natural population density of this species for comparison with densities from previous studies in fragmented and secondary habitat. Also more genetic studies should be made on the northern and southern populations of *C. oenanthe* to better understand the conservation needs of different morphs.

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Occurrences of the Golden-headed Lion Tamarin (*Leontopithecus chrysomelas*) above 500 Meters in Southern Bahia, Brazil and Implications for Conservation Planning

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Abstract: The golden-headed lion tamarin, *Leontopithecus chrysomelas*, was formerly thought to range below 300–400 m above sea level, because of changes in forest physiognomy and lack of resources at higher elevations. We document four cases (from two studies) of *L. chrysomelas* ranging above 500 m, and investigate the behavior of two groups that ranged from 100 to 700 m. We discuss the possibilities that 1) resources may be more abundant at higher elevations than previously thought, 2) a shift may have occurred in the species elevation-use patterns in response to forest loss and degradation at lower elevations, and that 3) golden-headed lion tamarins require low elevations for access to resources but use higher altitudes to travel between lower lying areas. Understanding exactly how *L. chrysomelas* uses higher elevations and the limits of its upper ranging patterns has significant conservation implications for this endangered species. Even without being able to definitively ascertain that golden-headed lion tamarins are able to settle in stable home ranges at higher elevations with adequate resources for breeding and survival, they certainly move through these habitats. We suggest, therefore, that slopes and ridge-tops should be taken into account as corridors to be preserved for gene flow in the otherwise highly fragmented *L. chrysomelas* metapopulation.

Key words: Altitudinal limit, golden-headed lion tamarin, *Leontopithecus chrysomelas*, Callitrichidae, forest connectivity, habitat suitability, Neotropics, resource limitation

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Introduction

The golden-headed lion tamarin (*Leontopithecus chrysomelas*) inhabits wet coastal and inland semi-deciduous forests in the northern Atlantic forest, extending through southern Bahia and, in the past, northwest Minas Gerais (Pinto and Rylands 1997; Raboy *et al.* 2010). It is classified as Endangered on the IUCN Red List due to habitat loss and fragmentation resulting from conversion of forest and shade-cocoa agroforest to cattle pasture or other agricultural crops. It was believed that *L. chrysomelas* inhabited altitudes mostly below 300 m above sea level (Coimbra-Filho 1969; Hershkovitz 1977; Rylands *et al.* 1993). Pinto and Rylands (1997) found *L. chrysomelas* as high as 400 m but supposed it improbable that *L. chrysomelas* would use elevations higher than 500–550 m because of changes in climate, floral communities and forest physiognomy. Areas in the *L. chrysomelas* geographic distribution include elevations up to 1,100 m (Fig. 1). The question thus remains, to what extent (altitudinal limit, frequency and type of use) do *L. chrysomelas* use the higher elevation habitats? The golden lion tamarin (*L. rosalia*), another coastal, but more southerly species, has now been found at elevations of up to 550 m (Kierulff and Rylands 2003). The black lion tamarin (*L. chrysopygus*), occurring on the inland plateau of the state of São Paulo, has been recorded at elevations of 700 m (Coimbra-Filho 1970) and 900 m (C. Knogge pers. comm.).

Here we report on the occurrence of *L. chrysomelas* in areas above 500 m on four occasions in different areas of their distribution. We also present a frequency histogram of elevation use from two study groups followed at higher elevations. We discuss reasons why *L. chrysomelas* might be seen at higher elevations and the conceptual implications of higher-elevation use for the development of habitat and landscape models implemented to assist in conservation planning for this species.

Methods

We compiled results from two different studies conducted by the authors in southern Bahia: the "GHLT Connection" and the "Cabruca Project." Researchers in the GHLT Connection conducted a survey of *L. chrysomelas* throughout the species' known historic distribution. The area, shown as the polygon outlined in black in Figure 1, included forests between the Rio de Contas and the Rio Jequitinhonha, from the coast westward toward the region of the rios Gongoji, Acará, Catolé Grande and Ribeirão do Salto. Researchers in the Cabruca Project studied the behavior and ecology of *L. chrysomelas* groups in shade-cocoa ("cabruca") agroforest. The Cabruca Project was carried out in two phases. The first was a survey of the shade-cocoa region in the east of the range of *L. chrysomelas* to select study sites, and the second involved the study of radio-collared groups of *L. chrysomelas* in the study locations chosen. *L. chrysomelas* groups were followed on multiple days in the municipalities of Camacã, Una, Ilhéus, Jussari and Arataca.

The two projects implemented varying overall experimental designs. The GHLT Connection surveyed forest patches selected by stratified random sampling between November 2005 and November 2007 using playback methods outlined in Raboy *et al.* (2010). When *L. chrysomelas* were sighted, a GPS point was taken. For the most part, elevations higher than 400 m were not sampled, presuming *L. chrysomelas* would not be found in these areas, but occasionally points along transects reached these elevations and higher. The Cabruca Project first surveyed for possible long-term monitoring sites between June and August of 2006 and 2007 based on results from the GHLT Connection, word of mouth regarding possible locations of *L. chrysomelas,* and additional playback work. Following that, selected *L. chrysomelas* groups were monitored with radio-telemetry between April 2008 and September 2009. Two of the seven study groups ranged in areas with elevations above 500 m. At 20-min intervals, a group's geographic position and altitude were recorded using a GPS device. UTM coordinates were collected using Corrégo Alegre datum (UTM Zone 24L) for both projects. The altitude of observations was determined by measuring elevation at the location of observation with the GPS altimeter and by cross referencing UTM coordinates (re-projected from the Corrégo Alegre datum to South American 69) with a Shuttle Radar Topography Mission (SRTM) elevation map of the study region (South American 69; data courtesy of NASA/NGA/USGS at http://www2.jpl.nasa.gov/srtm/).

For the first part of our investigation, we noted all observations from each of the two studies documenting *L. chrysomelas* above 500 m. We subsequently used the results of the Cabruca Project to determine histograms of elevation use for the two high-elevation study groups of *L. chrysomelas*. For this we determined the number of 20-minute observations that occurred in each 100 m altitude class to ≥700 m.

Results

We registered *L. chrysomelas* above 500 m at four different localities in three different municipalities of Bahia (Fig. 1):

1) *Floresta Azul (from GHLT Connection).* Two individuals were seen at 633 m (cross referenced at 600–700 m), responding to playback calls at the border between shade-cocoa and secondary forest. The group later moved to even higher altitude, although it was not possible to register a GPS point. 426166 E 8345747 N at maximum altitude measurable.

2) *Arataca (from Cabruca project - site selection phase)*. A group of four individuals was recorded at 515 m (cross referenced at 400–500 m but <80 m Euclidean distance from the 500 m contour) in primary forest. 463817 E 8319996 N.

3) *Arataca (from Cabruca Project - monitoring phase)*. A group of eight individuals including two infants (approximately one month old) were observed using a maximum altitude of 551 m (cross referenced at 500–600 m) in primary forest. 455530 E 8323006 N at maximum altitude observed.

4) *Camacã (from Cabruca Project - monitoring phase).* Two males were observed at a maximum altitude of 650 m (cross referenced at 600–700 m) in primary forest. 439756 E 8302606 N at maximum altitude observed.

The majority of the 20-minute observations for the Cabruca Project for one reproductive group ("Bem Te Vi") were in the 300–400 m elevation category (Fig. 2). On two of 14 days of observation, the group used altitudes above 500 m. For another group (two males; "São José"), the majority of observations were also in the 300–400 m elevation category, although the two males used five elevation classes (from 200 m to 600 m; Fig. 2). On three of seven days of observation they ranged to altitudes above 500 m. On one of those days, individuals in the São José group spent the entire day above 400 m in cabruca and primary forest, using a sleeping hole also above 400 m. Both groups of *L. chrysomelas* used slopes spanning at least four elevation classes or 400 m differential from highest to lowest observations.

Discussion

We documented four *L. chrysomelas* groups in different geographic regions using forests at 500–700 m altitude, the highest altitudes yet published for the species. Our findings imply several possibilities in relation to the previous suggestion that lion tamarins use only lower elevations. First, the hypothesis that resources are inadequate at higher elevations may be incorrect for the levels at which *L. chrysomelas* were found. In a study focusing on the avifauna of southern Bahia, Silveira *et al.* (2005) indicated that the vegetation became markedly stunted at approximately 800 m across their study sites in the Serra dos Lontras and Javi ranges. Up to this point, the forest still comprised tall trees and bromeliads (Silveira *et al.* 2005) and, at least in physiognomic terms, might be favorable to lion tamarins from what we know of their needs. In a botanical inventory of three montane areas in southern Bahia, Amorim *et al.* (2009) recorded 1,129 plants species at altitudes 300 to 1080 m above sea level. Seventeen species on this list were also present and classified as "extremely valuable" on a list of key resource species for *L. chrysomelas* by Oliveira *et al.* (2010) from a lower-lying forest (<100 m altitude). An additional 25 species were listed as "key" (useful but to a lesser degree than the "extremely valuable"; Oliveira *et al.* 2010). Amorim *et al*. (2009) also recorded high bromeliad diversity above 400 m. Golden-headed lion tamarins forage for animal prey most commonly in bromeliads (Oliveira *et al.*

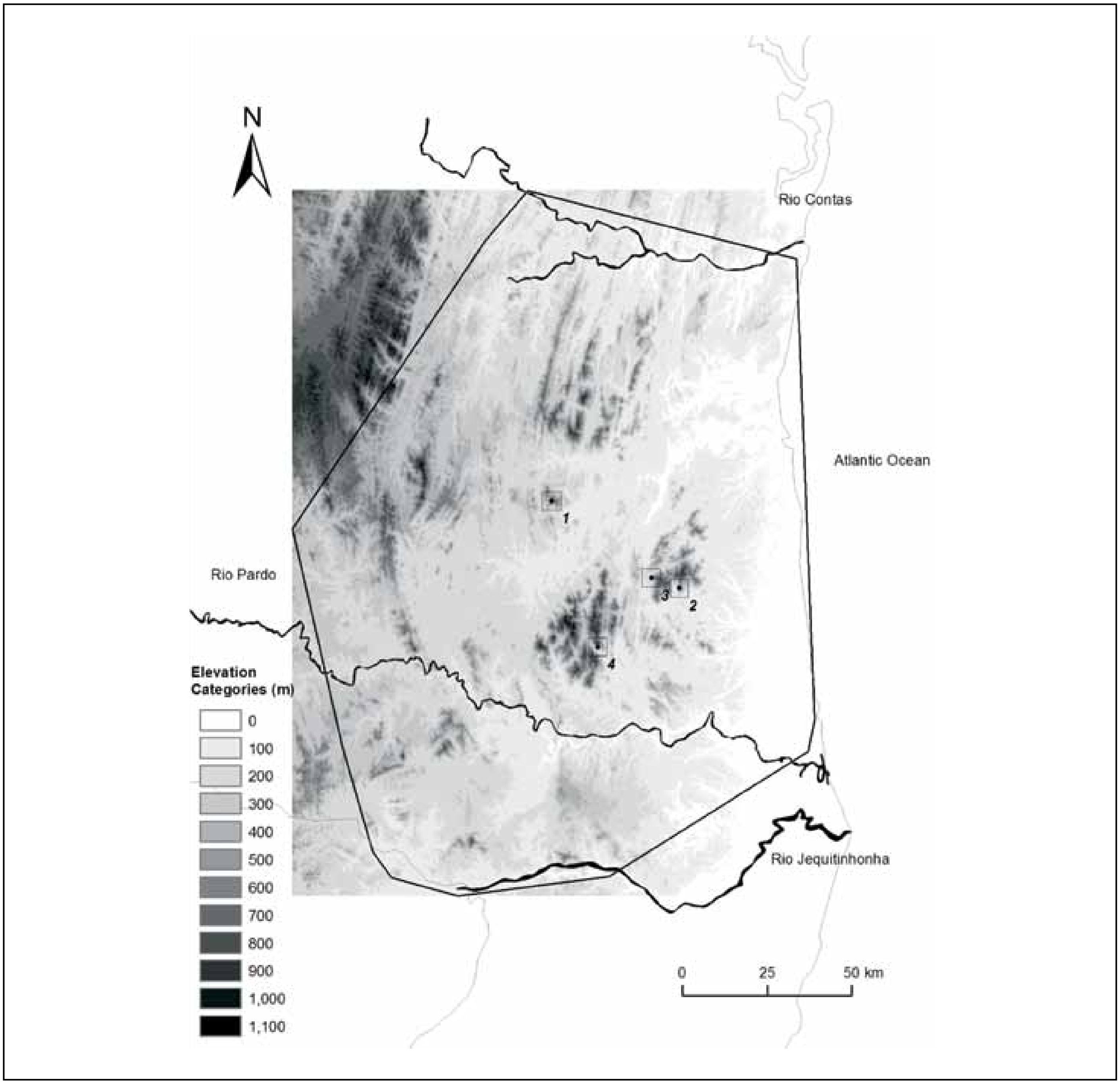

Figure 1. Elevation map of southern Bahia. A light grey line delineates the boundary of Bahia state. The black polygon represents the former distribution of *L. chrysomelas* and the area sampled for the GHLT Connection Project (Raboy *et al.* 2010). The four *L. chrysomelas* sightings above 500 m are shown by the points outlined in squares.

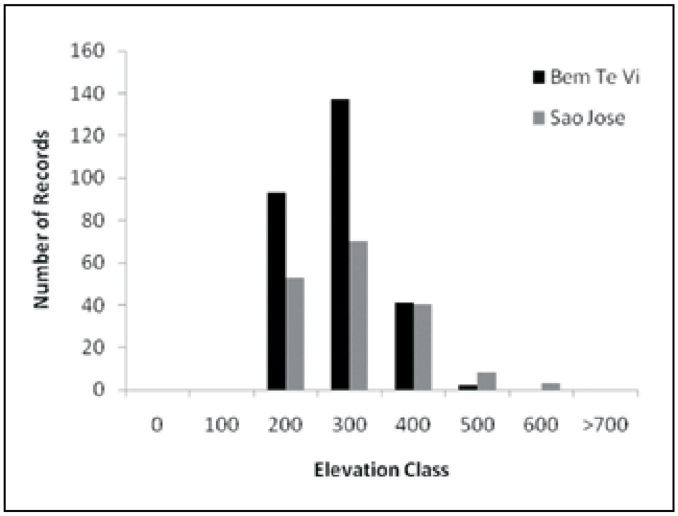

Figure 2. Elevational distribution of observations from two groups of *L. chrysomelas* in the Cabruca Project.

2011; Raboy and Dietz 2004). We documented *L. chrysomelas* above 500 m at two locations of the Amorim study. The results from Silveira *et al.* (2005), Amorim *et al.* (2009), and the Cabruca Project documenting golden-headed lion tamarin groups eating and sleeping above 400 m are suggestive that *L. chrysomelas* might have adequate resources at these and higher elevations.

Second, a shift may have occurred in the species elevation-use patterns in response to anthropogenic change in the region, and *L. chrysomelas* could be using higher elevations despite their poorer resources. Kierulff and Rylands (2003) suggested that the presence of *L. chrysomelas* above 500 m in the Serra do Mar in the state of Rio de Janeiro was the result of deforestation at lower levels that had pushed populations into more mountainous areas. Groups were seen at these higher elevations but near to houses where they had access to cultivated fruits such as bananas. Silveira *et al.* (2005) believed that extensive deforestation at lower elevations also explained the presence of some bird species found in Bahia at altitudes higher than documented in other locations. Historical evidence of the absence of lion tamarins in higher elevations currently used by them would indicate a shift towards higher elevation, but this information does not exist. Comparative studies of foraging and reproductive success of *L. chrysomelas* ranging exclusively at higher and at lower elevations along with corresponding phenological studies to estimate food availability would help elucidate the patterns in elevation use seen in this species.

With the exception of the studies we have mentioned, little information exists indicating the effect of altitudinal gradient on potential *L. chrysomelas* resources in southern Bahia. Other callitrichid genera have been documented using higher elevations in the Atlantic forest. *Callithrix geoffroyi,* also thought to be a lowland species (500 m; Passamani and Rylands 2000; Rylands and Faria 1993) with a similar diet to lion tamarins (except, principally, its exploitation of plant exudates when fruits are scarce), has been found in the Estação Biológica de Santa Lúcia, a reserve ranging from 550–950 m in Espirito Santo (Passamani *et al.* 2000) and at 1274 m in the Serra do Cipó National Park, Minas Gerais (Oliveira *et al.* 2003). Pinto *et al.* (2009) found that elevation was one of the five most important predictors of species density for three (*Brachyteles*, *Cebus* and *Callithrix*) of five focal species in a study of primates (including *Alouatta*, and *Callicebus*) throughout four Brazilian states: São Paulo, Rio de Janeiro, Minas Gerais and Espírito Santo. For *Brachyteles*, *Cebus* and *Callithrix*, the relationship between species density and elevation was negative, but elevation was less consistent as a predictor of density for all five species as compared to precipitation and temperature (Pinto *et al.* 2009).

Sightings of *L. chrysomelas* groups in higher altitudes do not necessarily mean that they use resources or reproduce in these areas. A third explanation is that they continue to be low-elevation species and only use higher-altitude forests for travel or dispersal, traversing slopes and peaks with limited or absent resources for the same reasons they cross open fields (B. Raboy pers. obs.). In the GHLT Connection, we observed that higher elevation forests tended to be better preserved than many of those in lower elevations. Summits at higher elevation in the west often stood as forest islands surrounded by cattle pasture. The steeper terrain and rise in elevation decreases its accessibility or suitability for certain forms of agriculture. Moreover, Brazilian legislation (Forestry Code/Federal law 4771/65 and CONAMA resolution 303/02) considered areas of steep terrain slopes (>45 degrees), hill and mountain tops (above 2/3 height in relation to the base) and high altitude (>1800 m) as Areas of Permanent Protection (APP; CONAMA 2002). APPs must preserve the original native vegetation and may not be used for production (Sparovek *et al.* 2010). Although *L. chrysomelas* resource quality has not been quantified in these areas, forested hilltops certainly provide *L. chrysomelas* with cover and protection from predators.

Increasing the known upper elevational limit to which *L. chrysomelas* finds resources, reproduces or travels within has implications for conservation planning in that it increases the available habitat. Assuming the higher-elevation habitat is suitable for finding resources and breeding, it provides refugia from the degradation and fragmentation of the lowland forests. If high elevation forests serve only as a conduit — a corridor — for dispersal and gene flow between lower-lying populations, this still has strong conservation implications, increasing the potential functional connectivity of existing fragments. Increased connectivity facilitates gene flow in the metapopulation, which is at present extremely fragmented (Raboy *et al*. 2010; Zeigler *et al.* 2010).

Prior conservation modeling predicting future *L. chrysomelas* abundance excluded the possibility that *L. chrysomelas* used forest above 400 m. Holst *et al.* (2006) conducted a Population and Habitat Viability Analysis (PHVA) for populations of *L. chrysomelas* in two areas containing high elevations — the Serra do Baixão and Serra das Lontras.

While the estimated overall areas were 32,089 ha for Serra do Baixão and 8,015 ha for Serra das Lontras, the areas deemed suitable for *L. chrysomelas* were only 13,782 ha and 1,668 ha respectively, principally due to the large amount of forest above 400 m elevation in these locations. If *L. chrysomelas* uses elevations greater than the upper limit of 400 m for maintaining territories and breeding, the predicted outcomes for population size and probability of maintaining genetic diversity in those locations could be considerably underestimated. Recent work with howler monkeys (*Alouatta pigra*) in cloud forest of Guatemala indicated use of much higher altitude than previously thought. The authors suggest these regions will become important for species conservation and must be included in updated estimates of the species range (Baumgarten and Williamson 2007).

Superimposing a reclassified elevation map (0–300 m, 300–500 m, 500–700 m and >700 m) on a forest cover map of the *L. chrysomelas* range elaborated by Zeigler *et al*. (2010), we determined that forested areas under 500 m in the *L. chrysomelas* range (880,179 ha) represented 91.2% of the total forest cover including all elevations (965,861 ha; Fig. 3). Forested areas between 500 m and 700 m were 6.2% and those

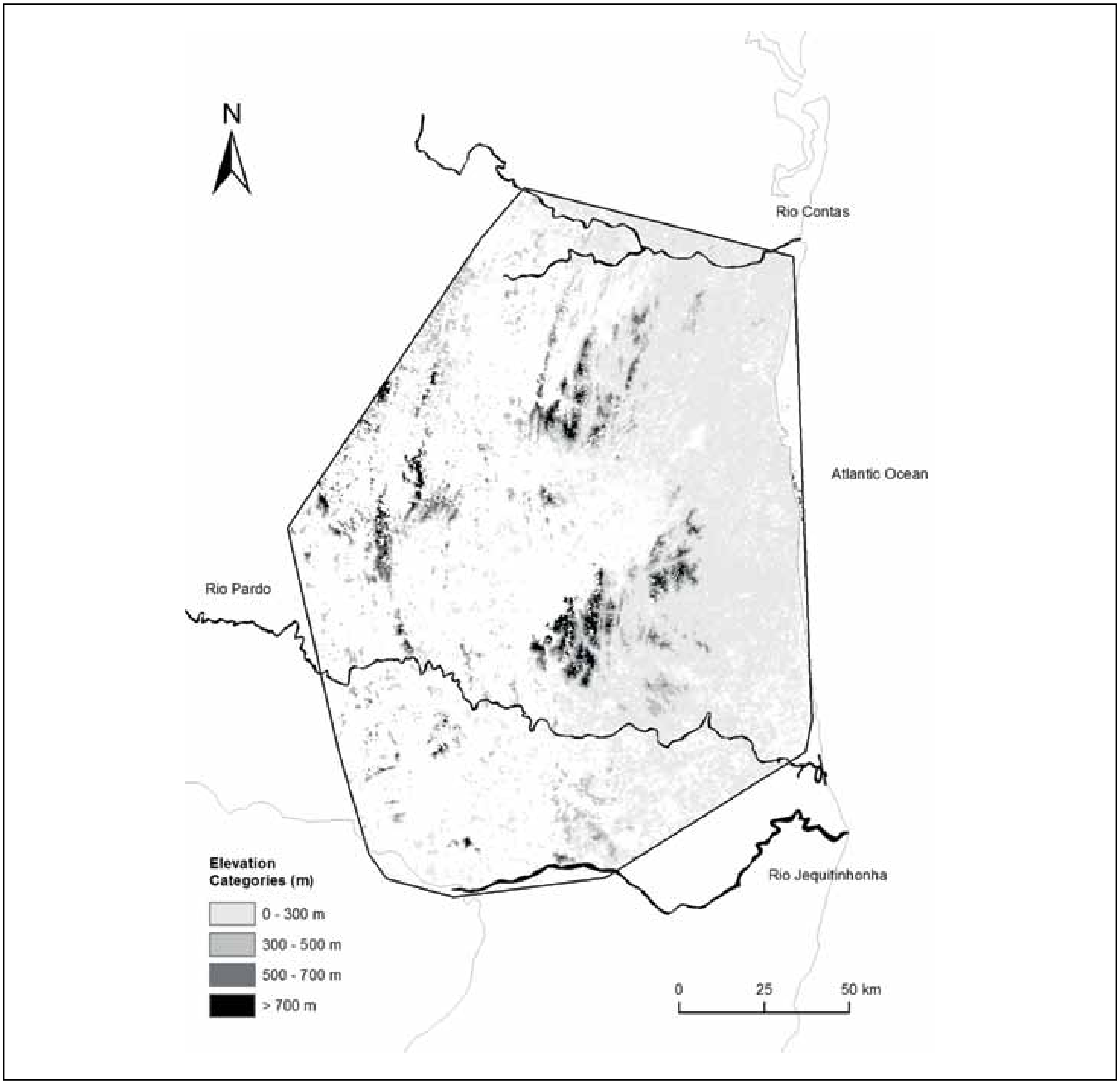

Figure 3. Map showing the remaining forest in the *L. chrysomelas* distribution by four elevation classes. Forest cover was determined by Sara Zeigler, based on interpretation of 2007 Landsat images (see Zeigler *et al*., 2010 for more details).

at elevations above 700 m were 2.6% of the total forest cover. Thus, the additional area gained, considering all forest up to 700 m as suitable for *L. chrysomelas* (rather than the <500 m model), increases potential forest for the species by 6.8%.

Functional connectivity also increased slightly, particularly north of the Rio Pardo, when forest at elevations above 500 m could serve as corridors for dispersing *L. chrysomelas* (S. Zeigler unpubl.). While high elevation areas make up only a small portion of the *L. chrysomelas* range, the location of these areas is significant. Many of them are located centrally in the *L. chrysomelas* distribution (Fig. 3) in areas that currently harbor *L. chrysomelas* and other threatened biodiversity (SAVE Brasil *et al.* 2009), such as those analyzed in the PHVA. These regions are regarded as having significant conservation potential as part of a network of reserves recently created or proposed (SAVE Brasil *et al.* 2009). Floresta Azul (Sighting 1) is within the Serra dos Barbados range that rises to approximately 800 m, with cabruca forest occurring up to 700 m. The region of Arataca where *L. chrysomelas* was found (Sightings 2 and 3), is part a chain of mountains that includes the Serra das Lontras, the Serra dos Quatis and the Serra Javi where the maximum altitude is nearly 1,000 m. Cabruca is prevalent up to altitudes of 600 m. The region of Camacã where *L. chrysomelas* was found (Sighting 4) is located in the Serra do Baixão chain (west of Lontras) that rises up to 900 m and is composed of a mosaic of vegetation ranging from open pasture to mature forest. Cabruca is a habitat known to be used by *L. chrysomelas* and provides suitable resources throughout the species' range (Oliveira *et al.* 2010, 2011; Raboy *et al.* 2010).

It is evident that *L. chrysomelas* can be found in higher elevations than previously thought, though exactly how they use these areas is still unclear. While observations of *L. chrysomelas* above 500 m are still seemingly rare, it is important to note that the two projects assessed in this paper for the most part avoided sampling for *L. chrysomelas* in higher altitude areas presuming the species would not be present. We predict that future systematic sampling for *L. chrysomelas* in elevations of 500 m to 700 m will yield a greater number of sightings than was documented from our *ad libitum* visitation of this elevation. Forested slopes and ridges serving as corridors (at least up to about 600–700 m) may greatly contribute to increasing the connectivity of the *L. chrysomelas* metapopulation and should be investigated further. Specifically, future studies are necessary to evaluate what limits the use of higher elevations by *L. chrysomelas*, what is truly "too high" for lion tamarins, and how ecological parameters (home range size, habitat use, sleeping site use and dispersal patterns) and social and demographic characteristics (group size, composition and biomass) of *L. chrysomelas* vary by elevation.

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Subspecific Variation: An Alternative Biogeographic Hypothesis Explaining Variation in Coat Color and Cranial Morphology in *Lagothrix lugens* (Primates: Atelidae)

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Abstract: In this study, I examined the skull morphology of three color phases of the Colombian Woolly Monkey *Lagothrix lugens* (Primates: Atelidae). Collecting localities of museum specimens were investigated through GIS-based modeling techniques to test for geographical and ecological patterns in *L. lugens* populations. Statistical analyses conducted on 28 cranio-mandibular measurements, in combination with the assessment of discrete characters, indicated that *L. lugens* consists of three geographic groups. The morphotype from the highlands of the Central Cordillera (>2,000 m altitude) matches in all characters the original description of *L. lugens*. There is a distinct morphotype from the lowlands of the northern Amazon (Department of Caquetá) and another from the piedmonts of the eastern versant of the Colombian Andes and the isolated mountains of the Serranía de la Macarena, herein recognized as new subspecies. The presence of an intermediate form between highland and lowland divergent lineages is also interpreted as indication of effective hybridization in a narrow contact zone at the Macizo de Garzón in the southernmost range of the Eastern Cordillera.

Key Words: Colombia, color variation, contact zone, *Lagothrix* races, skull morphology

Resumen: En este trabajo, se evaluó estadísticamente la morfología craneal de especímenes que representan tres fases de color, previamente identificadas en el primate endémico de Colombia *Lagothrix lugens* (Primates: Atelidae); al tiempo, la variación ecológica asociada a las localidades de colecta del material analizado fue investigada para probar la existencia de estructura ecológica y/o geográfica entre poblaciones de *L. lugens* mediante la aplicación de técnicas de modelamiento basadas en SIG. Los análisis estadísticos conducidos sobre 28 medidas cranio-mandibulares, en combinación con la evaluación de caracteres discretos, indicaron que la morfología craneal de *L. lugens* esta subdividida en tres grupos geográficos que incluyen un morfotipo de las tierras altas de la Cordillera Central de Colombia (>2,000 m) que coincide con todos los caracteres en la descripción original de *L. lugens*, y dos variantes geográficas que son presentadas en este estudio: un morfotipo de las tierras bajas de la Amazonía del departamento del Caquetá y un morfotipo de los piedemontes orientales de los Andes de Colombia y el sistema montañoso independiente de la Serranía de la Macarena, reconocidos en este trabajo como nuevas subespecies. Finalmente, se interpreta la presencia de una forma intermedia entre linajes divergentes de las tierras altas y bajas como indicación de hibridación en una zona de contacto estrecha en la unidad geológica del Macizo de Garzón al extremo sur de la Cordillera Oriental Colombiana.

Palabras clave: Colombia, morfología cranial, razas de *Lagothrix*, variación en color, zona de contacto

Introduction

Woolly monkeys in the genus *Lagothrix* are widely distributed in South America, occurring in distinct ecosystems from the Amazon basin to the piedmonts and highlands of the Andes of Venezuela, Colombia, Ecuador, and Peru (Fooden 1963; Groves 2001; Defler 2004). The genus presently contains four species: *L. lagothricha* (Humboldt 1812) in the Amazon and southern Orinoco basins of Brazil, Colombia, Ecuador, Peru and Venezuela; *L. cana* (É. Geoffroy 1812) with two subspecies, *L. c. tschudii* Pucheran, 1857, in the Andes and associated piedmonts of southern Peru, and *L. c.*

cana in the lowlands of the Amazon basin of Peru and Brazil; *L. poeppigii* Schinz, 1844 in the western Amazon and the Andes of Peru and Ecuador; and *L. lugens* Elliot, 1907, which has a wide ecological range from the lowlands of the Colombian Amazon, the eastern piedmonts of the Eastern Cordillera, as well as the highlands of the Central and Western Cordilleras of the Colombian Andes (Fooden 1963; Groves 2001; Defler 2004; Ruiz-García and Pinedo-Castro 2010).

Fooden (1963) identified three color phases of *L. lugens*, two of them quite distinct; one from the highlands of the Andes and the isolated Serranía de la Macarena, and the other from the lowlands of the department of Caquetá. Fooden (1963) described a third color phase represented by three individuals with an apparently restricted distribution. Although he used the subspecific epithet *lugens* for populations of *L. lagothricha* occurring north of the lower Río Guayabero (Defler 2004), only highland specimens from above 2,000 m matched the description of *L. lugens* Elliot 1907. The presence of different color phases identifying populations from ecologically contrasting habitats poses the alternative possibility that they represent independent evolutionary lineages within *L. lugens*. The presence of geographically restricted divergent specimens can also be interpreted as evidence of a contact zone between highland and lowland morphologically divergent taxa. Herein, these two hypotheses are tested through cranio-mandibular characterization of the three color phases described by Fooden (1963) and ecological analyses of their geographic ranges.

Materials and Methods

Specimens analyzed

This study was conducted in the mammal collection of the Field Museum of Natural History (FMNH), Chicago, Illinois, which holds the second largest and most geographically representative series of specimens in the genus *Lagothrix*, including all currently recognized taxa. It has the largest series of *L. lugens* of any museum, with 40 voucher specimens from nine localities, representing a significant portion of the known distribution of this taxon. All specimens analyzed were compared with the original description of *L. lugens* Elliot, 1907, in order to confirm their identity.

Morphometric variation among populations

To analyze the phenetic variation among *L. lugens* populations, a principal components analysis (PCA) was performed on 28 craniodental and mandibular measurements of adult individuals of both sexes. Males and females were analyzed separately to account for sexual dimorphism (males n=18; females n=10) (see Appendix I). The age of the specimens was estimated based on the presence of an entirely erupted and functional dentition, as well as completely fused spheno-occipital and/or ethmoid sutures.

Measurements in the present analysis included: greatest length of skull (GLS); braincase length (BCL); condylobasal length (CB); palatal length (PAL); zygomatic breadth (ZYG); braincase width (BCW); mastoid breadth (MB); braincase height (BCH); interorbital breadth (IO); anterorbital constriction breadth (AOC); intermalar width (IM); orbital height (OH); nasomaxillary height (NMH); malar foramen diameter (MFOR); left foramen ovale width (FOROVA-L*); right foramen ovale width (FOROVA-R*); length of upper molar row (MR); length of upper premolar row (PR); first molar width (M1W*); breadth across upper canines (CC); left tooth row (LTR); right tooth row (RTR*); mandible length (ML); ramus height (RM); maximum distance between the coronoid process and the angle of the mandible (MH2); mandibular process width (Md2); mandibular tooth row (MTR); and breadth across mandibular canines (CC-1). The measurements are shown in Figure 1 except for those with an asterisk. Principal components analyses were performed in the statistical package PAST available at <http://www.nhm.uio.no/norlex/past/download.html>.

Selection of informative variables

Based on the PCA factorial plane, correlated variables with the lowest loadings were eliminated (variables eliminated from the male dataset: BCL, ZYG, INT-ORB, OH, MFOR, FOR-OVA-R, M1W, CC, RM, Wd1, MTR; variables eliminated from the female dataset: CB, FOR-OVA-L, ZYG, MR, BCH, M1W, INT-ORB, CC, AOC, LTR, AIM, RTR, MAXNAS, RM, MFOR, Wd1, FOR-OVA-R, CC-1). For the remaining variables the change between simple and partial correlation matrices was evaluated and the variables in which the change was significantly different were also eliminated. In addition, values of a variance/covariance matrix from standardized data were calculated and the minimum number of variables to be included was determined based on their multiple correlation coefficient value. Finally, a PCA Cattel Scree plot test in the Statgraphics 15 package was used to determine the minimum number of variables to be used in the analysis (Fig. 2). Multiple correlation coefficients for the analyzed variables were calculated and ordered (low to high) selecting the number of variables suggested in the Scree plot. Variables eliminated from the male dataset were: MR, BCW, BCH, CC-1, AIM, FOR-OVAL-L, LTR. Variables eliminated from the female dataset were: PAL, MH2, MTR, ML, PR, BCW, MB)(Fig. 2). Selected variables in male (BCW, BCH, CC-1, LTR, MR, FOR-OVAL-L) and female (PAL, BCW, MB, PR, ML, MH2, MTR) datasets were tested for normality by the application of an Energy test in R mvnorm.etest for independent variables. Selected measurements for males are marked by a single asterisk (*) and for females by a double asterisk (**) in Table 1.

The geographic subdivision proposed for *L. lugens* populations among contrasting geographic locations was: i) highlands of the Central Cordillera of the Colombian Andes; ii) Eastern piedmonts of the Eastern Cordillera of the Colombian Andes, including the Serranía de La Macarena; and iii) Amazonian lowlands in the department of Caquetá. This subdivision was statistically assessed through a discriminant function analysis (DFA) in the statistical package Statgraphics 15 performed on the seven selected cranio-mandibular variables for males and females separately to account for sexual dimorphism (Fig. 2).

Geographic and ecological analyses

To characterize the collecting localities of the woolly monkey populations, a principal components analysis (PCAenv) was performed on four environmental variables (elevation, precipitation, and minimum and maximum temperature) derived from raster layers of the Bioclim dataset (Fig. 3). To determine the extent of suitable conditions for *L. lugens* and to test for the presence of i) natural barriers contributing to population isolation and ii) the presence

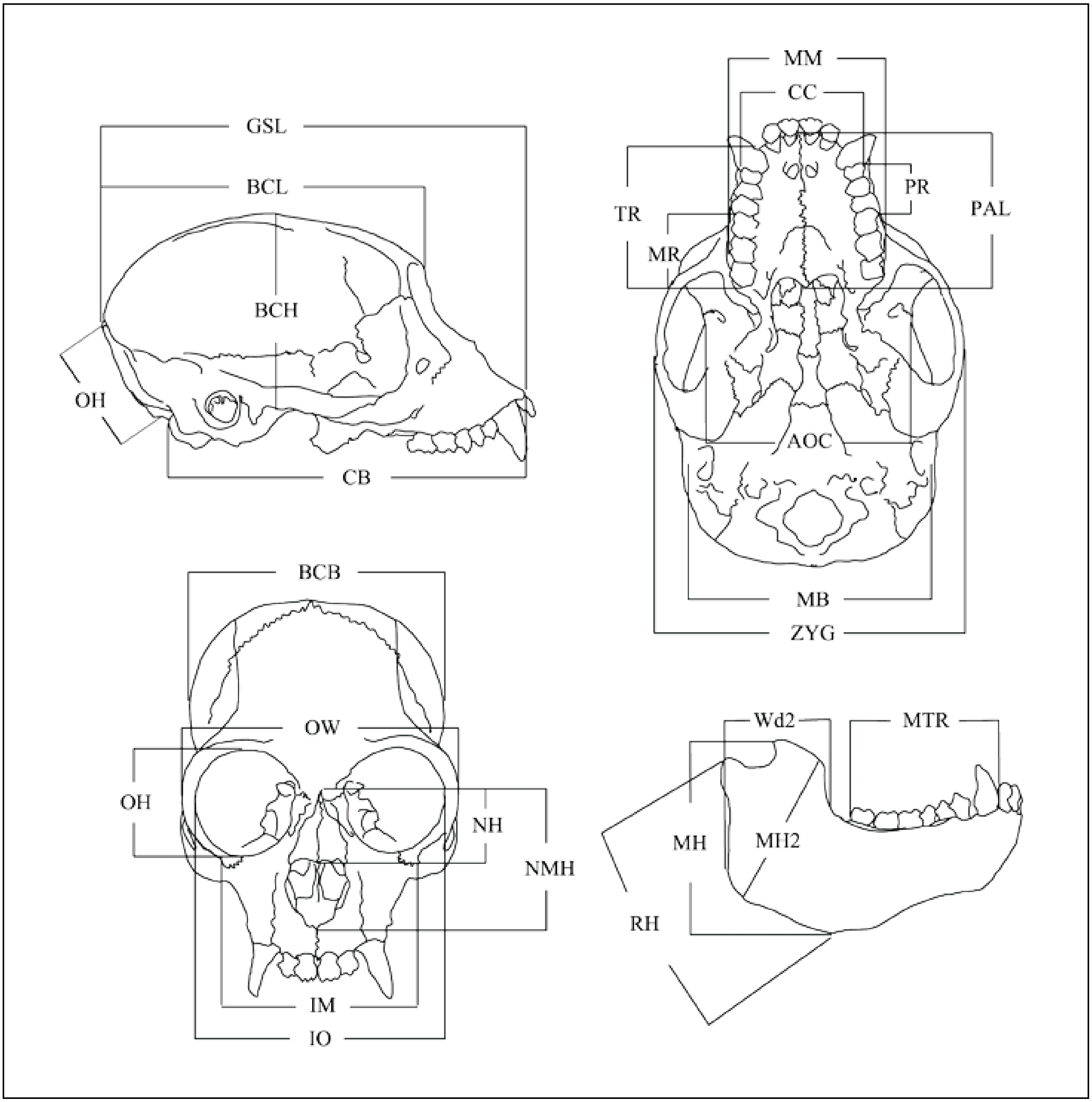

Figure 1. Visual representation of cranio-mandibular measurements analyzed in this work; abbreviations described as follows: Greatest length of skull (GLS); braincase length (BCL); condylobasal length (CB); palatal length (PAL); zygomatic breadth (ZYG); braincase width (BCW); mastoid breadth (MB); braincase height (BCH); interorbital breadth (IO); anterorbital constriction breadth (AOC); intermalar width (IM); orbital height (OH); nasomaxillary height (NMH); malar foramen diameter (MFOR), not represented; left foramen ovale width (FOROVA-L), not represented; right foramen ovale width (FOROVA-R) not represented; length of upper molars row (MR); length of upper premolars row (PR); first molar width (M1W), not represented; breadth across upper canines (CC); left tooth row (LTR); right tooth row (RTR), not represented; mandible length (ML); ramus height (RM); maximum distance between the coronoid process and the angle of the mandible (MH2); mandibular process width (Md2); mandibular tooth row (MTR); breadth across mandibular canines (MCC).

Table 1. Average and standard deviation of 28 craniodental measurements among groups identified in this work. Abbreviations are given in Figure 1.

***Lagothrix* ssp.**	**No.**		**GLS**	**BCL**	**CB**	**PAL (**)**	**ZYG**	**BCW (*, **)**	**MB (**)**
lugens	N=9 ♂	Avg	102.9	79.5	85.8	31.7	67.8	58.6	55.8
		StDv	3.2	2.2	3.2	1.7	3.9	0.8	1.3
	N=5♀	Avg	101.9	77.7	88.9	31.0	67.0	60.1	55.2
		StDv	1.8	0.7	5.1	1.6	0.9	1.5	1.9
sapiens	N=3♂	Avg	110.3	84.1	92.8	32.5	71.4	59.8	57.0
		StDv	3.9	2.7	3.8	0.4	4.6	1.4	0.5
	N=2♀	Avg	105.2	80.5	90.2	32.4	65.9	58.5	55.5
defleri	N=6♂	Avg	109.9	83.4	91.7	35.7	70.0	58.6	55.9
		StDv	3.3	2.2	2.7	2.3	3.7	1.4	1.4
	N=4♀	Avg	103.13	78.3	86.8	31.7	66.3	57.8	54.7
		StDv	4.4	4.2	2.2	1.0	1.3	1.6	2.7
			BCH (*)	**INT-ORB**	**AOC**	**AIM (*)**	**OH**	**MAXNAS**	**MFOR**
lugens	N=9 ♂	Avg	47.6	50.9	46.4	54.4	22.8	33.4	4.1
		StDv	1.8	2.3	1.1	2.7	1.4	1.9	0.9
	N=5♀	Avg	47.5	52.3	46.7	54.4	23.8	33.0	3.8
		StDv	1.1	0.9	1.1	1.0	1.1	2.5	1.0
sapiens	N=3♂	Avg	47.3	53.0	46.8	57.1	24.2	36.1	3.1
		StDv	0.4	2.5	2.0	3.3	1.6	1.6	0.8
	N=2♀	Avg	46.0	52.0	46.1	53.7	23.6	34.3	3.0
defleri	N=6♂	Avg	47.5	52.8	45.9	55.8	23.8	37.6	4.4
		StDv	0.9	2.0	1.3	2.1	1.0	1.1	0.9
	N=4♀	Avg	46.7	51.7	45.8	53.6	22.2	35.2	3.3
		StDv	2.8	1.2	1.5	1.5	0.6	2.6	1.0
			FOR-OVA-R	**FOR-OVA-L (*)**	**MR (**)**	**PR (**)**	**M1W**	**CC**	**LTR (*)**
lugens	N=9 ♂	Avg	4.0	4.0	13.9	10.6	6.1	28.2	30.2
		StDv	0.6	0.7	0.7	0.5	0.4	2.4	1.1
	N=5♀	Avg	3.8	4.0	15.6	11.8	6.6	26.7	30.7
		StDv	0.8	1.1	1.7	0.4	0.1	1.0	0.5
sapiens	N=3♂	Avg	4.3	4.4	14.7	10.9	6.3	30.1	31.5
		StDv	0.6	0.2	0.7	0.6	0.1	1.5	0.6
	N=2♀	Avg	3.7	3.8	15.1	10.8	6.8	27.1	31.0
defleri	N=6♂	Avg	5.4	5.3	14.7	11.2	6.3	29.2	31.6
		StDv	0.9	0.5	0.7	0.8	0.2	1.9	0.9
	N=4♀	Avg	5.4	5.6	14.5	10.8	6.2	27.1	30.9
		StDv	0.9	0.9	0.7	0.4	0.2	0.6	1.2
			RTR	**ML**	**RM**	**MH2 (**)**	**Wd1**	**MTR (**)**	**CC-1 (*)**
lugens	N=9 ♂	Avg	30.3	68.7	50.1	42.2	24.1	21.0	19.6
		StDv	0.9	3.4	5.2	5.3	2.1	1.7	1.4
	N=5♀	Avg	30.8	68.1	47.1	40.3	23.5	22.4	18.8
		StDv	0.7	0.7	3.2	2.0	1.0	0.4	0.6
sapiens	N=3♂	Avg	31.4	73.9	51.5	45.5	26.7	21.1	19.6
		StDv	0.55	4.0	1.8	3.2	2.2	0.4	0.4
	N=2♀	Avg	31.1	69.2	45.2	40.1	23.9	22.3	18.7
defleri	N=6♂	Avg	31.8	74.1	52.8	47.3	28.7	21.5	20.6
		StDv	0.7	3.6	4.7	4.4	2.9	0.6	0.4
	N=4♀	Avg	30.8	68.5	47.1	42.9	25.5	21.7	19.0
		StDv	1.3	2.4	1.2	2.6	1.3	1.4	0.6

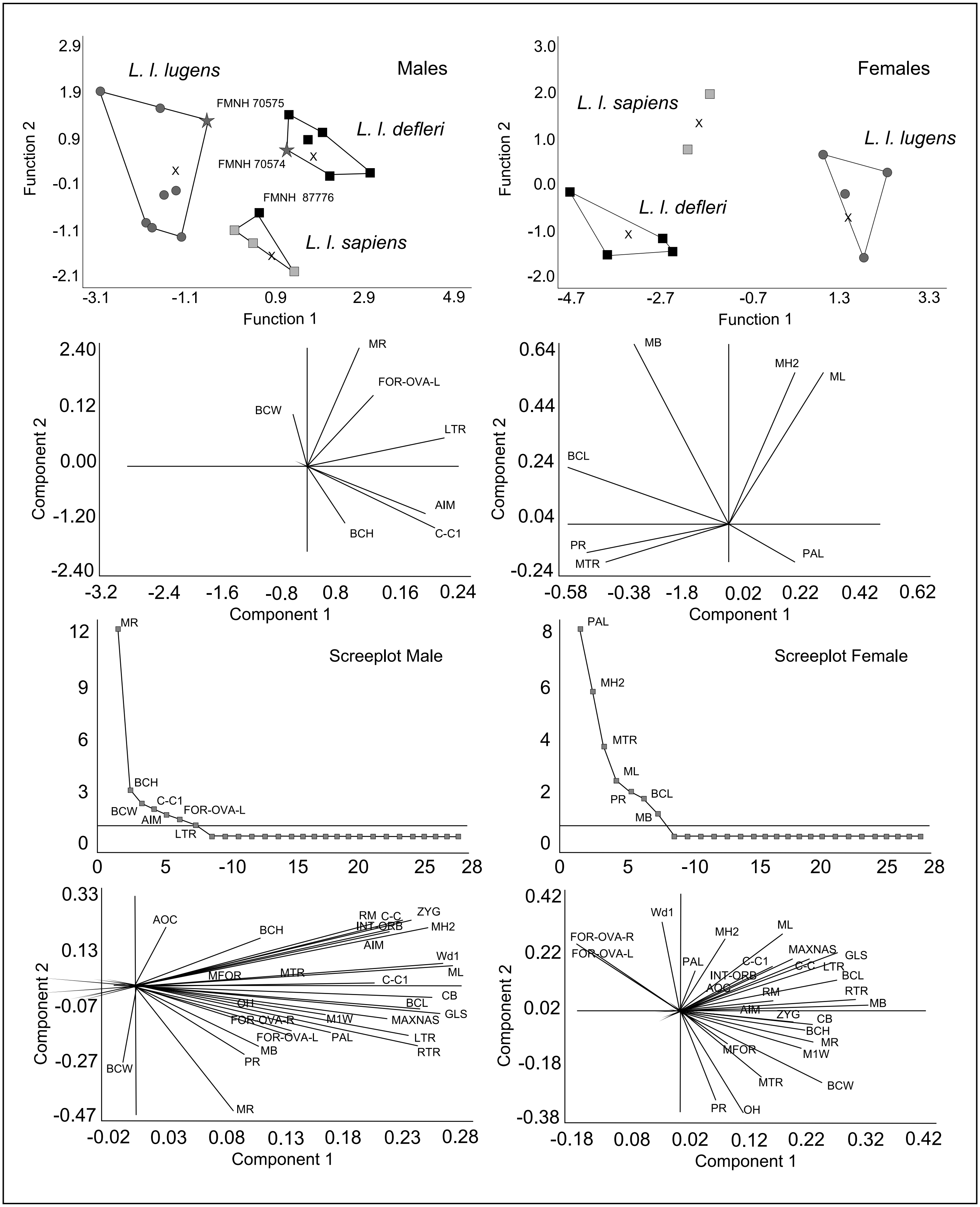

Figure 2. Discriminant function analysis (DFA) performed on seven selected craniodental variables for both male and female specimens, representing *L. lugens* populations from: 1) the lowlands of the northern Amazon in the department of Caquetá (gray squares), 2) highlands of the Andes (gray circles); and 3) the piedmonts on the eastern versant of the Eastern Cordillera and the Serranía de la Macarena (black squares) (first row); vectors of the seven selected variables in the principal components analysis (PCA) (second row); scree plot showing selected variables (third row); and preliminary PCA with the original variables (fourth row).

of potential routes of gene flow, a maximum entropy niche model (Maxent) was generated based on 19 collecting localities associated with museum voucher specimens reported by Fooden (1963) (nine of them included in the present work), following the protocols described in Phillips *et al.* (2006). Collecting localities of *L. lugens* used in the present analyses are described in Fooden (1963: pp.216–217).

In order to identify associations of environmental variables to the occurrence of *L. lugens*, a Pearson's multiple correlation test was performed between Maxent predictive values and values of 20 environmental variables derived from the Bioclim dataset in the statistical package SPSS 9.0. Descriptions of the environmental variables used in the geographic analyses of this work are available at <http://www.worldclim.org/bioclim>.

Results

Identity of specimens analyzed

Among the 28 analyzed adult specimens, 12 (43%) were characterized as Elliot's morphotype, matching the typical coloration attributed to *L. lugens* in Elliot's (1907) description of the species. They are referred to here as the "highland morphotype". Five specimens (18%) corresponded to the "lowland morphotype," and nine (32%) were identified as of the "piedmonts morphotype." Two specimens (7%) identified with catalogue numbers FMNH 70574 and FMNH 70575, from Aguas Claras, Huila, corresponded to an intermediate color phase between the color patterns typical of the lowland and highland populations. A detailed description of morphotypes and color phases is addressed in the "Discussion." Averages and standard deviations of cranio-mandibular measurements of identified divergent *L. lugens* morphotypes are presented in Table 1.

Normality test

Normality was proved at the 5% level of significance for both sets of variables (male and female datasets) in an Energy test of multivaried normality implemented in the statistical package R (data: males, estimated parameters, sample size 18, dimensions 7, replicates 999, E-statistic = 1.3772, *p value* = 0.09409; females, sample size 10, dimension 7, replicates 999, E-statistic = 1.2567, *p value* = 0.9259).

Principal Components Analysis (PCA)

In both PCAs (male and female datasets), the first three components accounted for most of the observed skull variation (PC1 = 36.9%, PC2 = 24.4%, and PC3 = 0% for males; and PC1 = 37.9%, PC2 = 27.6%, and PC3 = 17.1% for females) (Fig. 2). In the male dataset, MR, LTR, and CC-1, were the variables explaining most of the observed variation; while BCL, MB, and ML were the variables explaining most of the observed variation for the female dataset (Fig. 2).

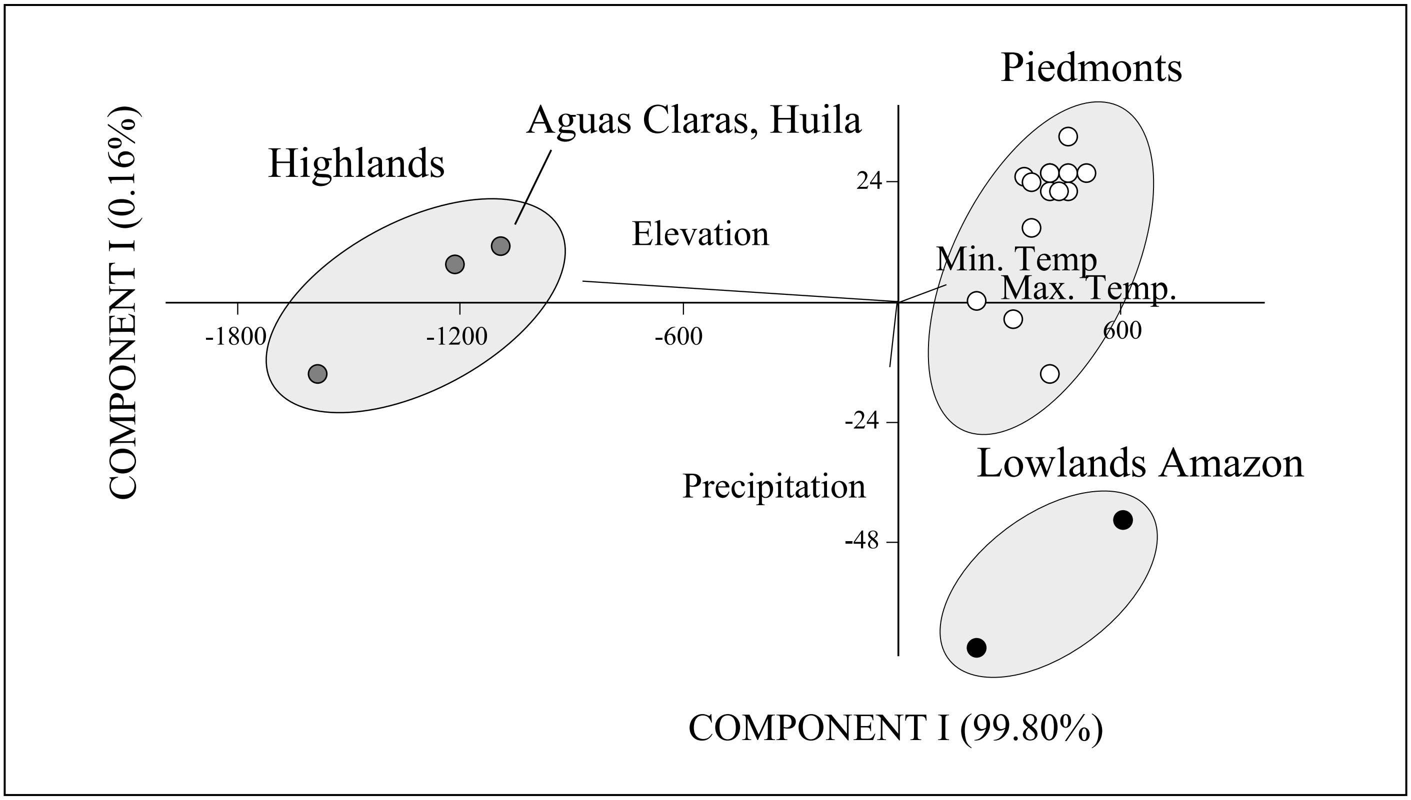

Figure 3. Principal components analysis performed on four environmental variables (elevation, precipitation, maximum temperature, and minimum temperature) associated with 19 collecting localities of *Lagothrix lugens*. Collecting localities from the highlands of the Central Cordillera (gray circles) were clearly differentiated from Eastern piedmonts localities (open circles), and from lowland localities in the Amazon (black circles).

Discriminant Function Analysis (DFA)

Female specimens from the three biogeographic regions were clearly discriminated in the DFA with 100% of specimens correctly assigned (Functions 1 and 2: Wilks' $\lambda = 0.046, 0.52$; $\chi^2 = 15.31, 3.17$; $P = 0.35, 0.7$) (Fig. 2). Male specimens from the three biogeographic regions were clearly discriminated in the DFA with 94.4% of specimens correctly assigned (Functions 1 and 2: Wilks' $\lambda = 0.188, 0.632$; $\chi^2 = 20.03, 5.49$; $P = 0.1293, 0.482$). Only two male specimens (FMNH 70574 from Aguas Claras, Huila, and FMNH 87776 from La Macarena, Meta) were incorrectly assigned (Fig. 2) (Table 2).

Collecting localities and niche modeling

Most of the ecological variation among the collecting localities analyzed was explained by the PC1 of PCAenv (99.8%) with higher loadings associated with elevation and precipitation (values of variance for elevation and precipitation: 99.78% and 0.24% respectively; Fig. 3B).

The Maximum Entropy model created for *L. lugens* (Fig. 4) failed to include all analyzed collecting localities within a single area of predictive values greater than 30%. Areas associated with high predictability (>60%) had a scattered distribution along the piedmonts of the Andes, with values greater than 80% restricted to the eastern Andes in the departments of Cundinamarca and Meta, including the Serranía de la Macarena. The Central Cordillera and the lowlands of the Amazon in the department of Caquetá were associated with lower predictive values (<40%). Finally, the distribution of *L. lugens* was positively and significantly correlated with precipitation (Pearson's correlation, $p > 0.001$: mean annual precipitation = 0.35; precipitation wettest quarter = 0.30; precipitation wettest month = 0.28).

Discussion

The stability of the alpha taxonomy of living New World monkeys, largely based on the contributions of Philip Hershkovitz in the decades of the 1950s, has experienced an extreme makeover (Rosenberger and Matthews 2008). From 67 recognized species in Napier (1976), the number of accepted platyrrhines has more than doubled at 139 (Rylands and Mittermeier 2009). The woolly monkeys, *Lagothrix* are not an exception. The last morphological revision of the genus, conducted almost half of a century ago by Fooden (1963), recognized just two species: the monotypic *L. flavicauda*, and *L. lagothricha* with four geographic variants: *L. l. cana*, *L. l. lagothricha*, *L. l. lugens*, and *L. l. poeppigii*. Groves (2001) not only resurrected the genus *Oreonax* Thomas, 1927 for the Peruvian Yellow-tailed Woolly Monkey (*O. flavicauda*), but also elevated to species rank the four subspecies of *L. lagothricha* and recognized two subspecies in *L. cana* (one from the highlands and one from the lowlands). Regardless of the debate on the validity and systematic placement of *Oreonax* (questioned by Rosenberger and Matthews 2008), the number of recognized independent lineages in *Lagothrix* has remained relatively stable. Two species of *Lagothrix* have been documented in Colombia: *L. lagothricha* and *L. lugens*. The former is a typical lowland species restricted to forested areas of the Amazon and Orinoco basins, northwest to an undetermined point in the Colombian department of Caquetá where it is replaced by *L. lugens* (see Defler 2004; Hernández-Camacho and Cooper 1976).

Lagothrix lugens evidently has a greater ecological range compared to other species in the genus (Fooden 1963; Ruiz-García and Pinedo-Castro 2010). It occurs across the lowlands of the northern Amazon, the piedmonts of the Orinoquia, as well as the highlands of the Central and Western Cordilleras of

Table 2. Classification table of Discriminant Analysis Function performed on the proposed *L. lugens* populations. 94.4% of the analyzed male specimens were correctly assigned. Only male specimen FMNH 70574, from Aguas Claras, Huila, and FMNH 87776, from La Macarena, Meta were incorrectly assigned and are marked with an asterisk.

Catalogue No.	Actual Group	High. Group	Highest value	Sq. Dist.	Prob.	2° High. Group	2° High. Value	Sq. Dist.
FMNH 70601	*L. l. sapiens*	*L. l. sapiens*	2855,41	0,792413	0,9395	*L. l. defleri*	2852,61	6,39719
FMNH 70604	*L. l. sapiens*	*L. l. sapiens*	2643,45	0,023887	0,8909	*L. l. defleri*	2640,79	5,35769
FMNH 70605	*L. l. sapiens*	*L. l. sapiens*	2654,32	0,541194	0,7630	*L. l. lugens*	2652,87	3,44328
FMNH 87775	*L. l. defleri*	*L. l. defleri*	2891,69	1,67249	0,9695	*L. l. sapiens*	2888,22	8,60618
FMNH 87776	*L. l. defleri*	*L. l. sapiens**	2734,85	0,637566	0,6813	*L. l. defleri*	2733,64	3,06494
FMNH 87777	*L. l. defleri*	*L. l. defleri*	2789,76	0,32858	0,9782	*L. l. sapiens*	2785,76	8,31237
FMNH 87781	*L. l. defleri*	*L. l. defleri*	2624,04	1,16378	0,9580	*L. l. lugens*	2620,43	8,39185
FMNH 92331	*L. l. defleri*	*L. l. defleri*	2722,23	0,271649	0,9144	*L. l. sapiens*	2719,84	5,0705
FMNH 92332	*L. l. defleri*	*L.l. defleri*	2669,13	0,167484	0,9569	*L. l. sapiens*	2665,77	6,88185
FMNH 70574	*L. l. lugens*	*L. l. defleri**	2682,16	0,407302	0,8841	*L. l. sapiens*	2679,67	5,37968
FMNH 70575	*L. l. lugens*	*L. l. lugens*	2634,23	0,190419	0,9217	*L. l. sapiens*	2631,67	5,30932
FMNH 70577	*L. l. lugens*	*L. l. lugens*	2604,86	1,67179	0,9317	*L. l. sapiens*	2602,23	6,92209
FMNH 70578	*L. l. lugens*	*L. l. lugens*	2623,03	2,03225	0,6432	*L. l. sapiens*	2622,42	3,24302
FMNH 70579	*L. l. lugens*	*L. l. lugens*	2590,16	1,7327	0,8761	*L. l. defleri*	2588,02	6,02033
FMNH 70580	*L. l. lugens*	*L. l. lugens*	2607,95	0,308933	0,9426	*L. l. sapiens*	2605,09	6,03392
FMNH 70585	*L. l. lugens*	*L. l. lugens*	2614,13	5,8484	0,9999	*L. l. defleri*	2604,67	24,7829
FMNH 70588	*L. l. lugens*	*L. l. lugens*	2684,56	1,94948	0,9938	*L. l. defleri*	2679,13	12,7944
FMNH 84550	*L. l. lugens*	*L. l. lugens*	2619,12	1,7559	0,9072	*L. l. sapiens*	2616,83	6,33834

the Colombian Andean system (Defler 2004). The 19 *L. lugens* collecting localities examined in this work represent nine biogeographic districts, as defined by Hernández-Camacho et al. (1992), that range from 50 to 3,000 m above sea level. Fooden (1963) documented three different color phases in the distributional range of *L. lugens*. Only one of the color variants matches all the characteristics of the specimen from the upper Río Magdalena (3,000 m above sea level) designated by Elliot (1907) as the holotype of *L. l. lugens*: "body stout, heavy, as in *L. lagothricha*, but color very different, black-purplish; fur thick, woolly; and a tail broad at base" (p.193). Fooden (1963) interpreted the observed coat color differences among *lugens* populations as clinal intraspecific variation. From my perspective, Fooden's (1963) interpretation was strongly influenced by assumptions in the Biological Species Concept (Mayr 1942). It is also important to mention that at the time of Fooden's revision hybridization among mammals was considered a rare event usually discarded from systematic analyses. As a result, Fooden (1963) retained the name *L. lagothricha lugens* for all populations north of the lower Río Guayabero.

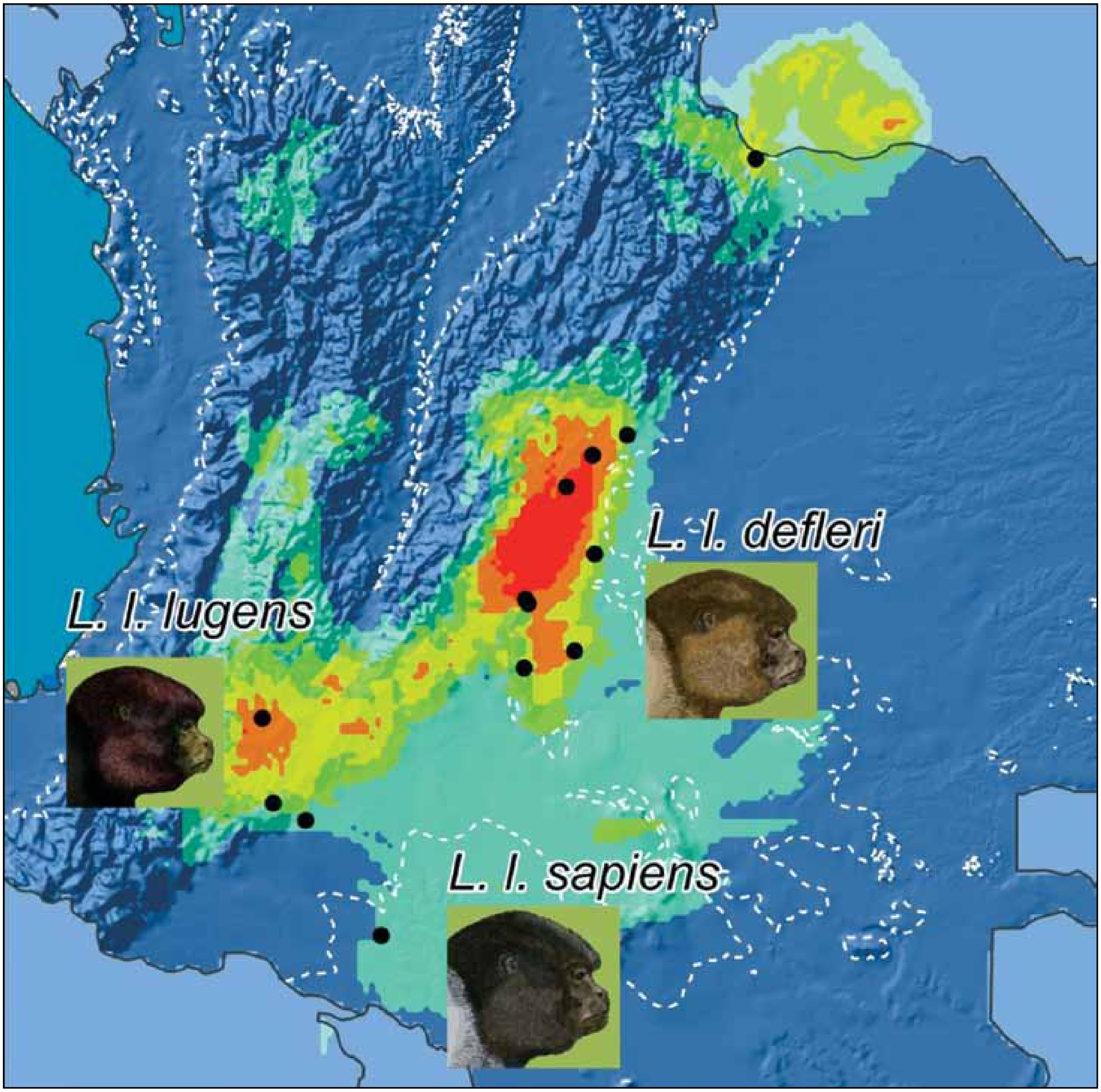

Figure 4. Predicted distribution for *L. lugens* derived from a Maximum Entropy modeling run for the 19 collecting localities of *L. lugens* analyzed by Fooden (1963) (black circles). Warm colors (red to yellow) represent probabilities greater than 50%. At 30% of predictability (aquamarine), the model succeeds in including all analyzed localities. Dashed line represents elevation of 250 m above sea level.

In my study, the skull morphology of the highland specimens, (matching all the characteristics found in Elliot's description of *L. lugens*) was clearly discriminated from lowland skulls in the DFAs of both males and females (Fig. 2). Colombian woolly monkeys from the lowlands have significantly larger skulls than the highland specimens. Lowland *L. lugens*, on the other hand, were divisible into two groups in both male and female DFAs as follows: 1) Amazon specimens, characterized by an overall silver coat color and a black cap ornate with a gray or silver mid-sagittal coronal stripe (a color phase also recognized by Fooden 1963); and 2) specimens from the piedmonts of the Eastern Cordillera and the Serranía de la Macarena, characterized by: i) a darker coloration in comparison with *L. lugens* specimens from the Amazon; ii) less defined cap and mid-sagittal stripe; iii) a larger body size compared to *L. lugens* from the highlands; iv) a shorter tail than *L. lugens* from the Amazon; and v) longer hair than in *L. lugens* from the Amazon. The above mentioned morphotype was interpreted by Fooden (1963) as a darker variant of *L. lugens* from the Amazon. In the male PCA, variables responsible for the differentiation among identified populations refer to the upper and lower molar tooth rows as well as canine separation (MR, LTR, and CC-1), all of them representing differences in dentition size; while females were differentiated by braincase length, mastoid breadth, and mandible length (BCL, MB, and ML), showing differences in skull size among identified groups. Fooden's third color phase corresponds to paler buffy-gray to brownish-gray primates, represented by one specimen from Consaya, Caquetá, and two specimens from Aguas Claras, Huila. Skull measurements in the specimen from Consaya did not differ significantly from other specimens from the same locality. On the other hand, although skulls from Aguas Claras, Huila, fell within the ranges of highland *L. lugens*, male specimen FMNH 70574 from this locality was misclassified as *L. lugens* from the Amazon in the DFA. Interestingly, specimen FMNH 7057, also from Aguas Claras, Huila, represented the most marginal point among highland samples in the DFA morphospace (Fig. 2). Aguas Claras, Huila, is part of the recently uplifted geologic unit of the Macizo de Garzón, located at the southernmost end of the Eastern Cordillera of the Colombian Andes, separating the lowlands of the Magdalena Valley from the lowlands of the Colombian Amazon and Orinoquia (Lundberg 1997). The area at the Macizo de Garzón encloses the lowest crossing points connecting the eastern and western versants of the Eastern Cordillera, and also constitutes the most likely location for intergradation between *L. lugens* from the eastern piedmonts and lowlands with individuals of *L. lugens* from the Central Cordillera of the Colombian Andes.

Ruiz-García and Pinedo-Castro (2010) examined the genetic variation of the mitochondrial marker COII for 26 putative Colombian *L. lugens* and concluded this taxon was polyphyletic encompassing higher genetic diversity than other putative species in the genus. Ruiz-García and Pinedo-Castro (2010) also mentioned that levels of genetic divergence of COII among *L. lugens* samples were lower than those between species of *Ateles* (Collins and Dubach 2000), implying subspecific designation for the observed genetic differentiation. The same authors highlighted high historical gene flow estimates within *L. lugens,* interpreted as evidence of effective hybridization between *L. lugens* and neighboring taxa, also exemplified by individuals originated from the breeding of *L. lugens* males with *L. lagothricha* females (Ruiz-García and Pinedo-Castro 2010: p.121). Interspecific breeding among primates such as *Lagothrix*, characterized by large groups with diurnal activities that involve extensive interspecific social interaction (Defler, 2004 and cited references in pages 358–359; Defler and Defler 1996) is likely to occur.

Hybridization has been documented in 26 of the 233 Old World primate species (Phillips-Conroy and Jolly 1986; Samuels and Altman 1986; Struhsaker *et al.* 1988; Watanabe and Matsmura 1991; Bynum *et al.* 1997; Evans *et al.* 2001; Wyner *et al.* 2002), even at the intergeneric level (Dunbar and Dunbar 1974; Jolly *et al.* 1997), and in eight of the 139 New World primate taxa (Coimbra-Filho *et al.* 1993; Cortés-Ortiz *et al.* 2007; Mendes 1997; Peres *et al.* 1996). At least two hybrid speciation events have been suggested among primates: *Macaca arctoides* (see Tosi *et al.* 2003) and *Rungwecebus kipunji* (see Burrell *et al*. 2009). A common aspect in all the above mentioned studies is the presence of individuals which exhibit some combination of characters (i) an intermediate or transgressive phenotype with respect to parental species, (ii) a restricted distribution or distribution within a vegetation zone (in allopatry or parapatry) from that of parental species, and/or (iii) isolation from parental species by either allopatry or assortative mating (e.g., allochrony or mate choice), characteristics shared by *L. lugens* specimens from Aguas Claras, Huila.

The Bateson-Dobzhansky-Müller genetic speciation model (Baker and Bradley 2006) states that the absence of effective mechanisms of sexual isolation and the presence of hybrid forms are not in full disagreement with speciation produced by temporal isolation of parental populations, accompanied by the fixation of characters in a process that can be reinforced by ecological differentiation. Results in this work have demonstrated the fixation of skull morphometric traits with a clear discrimination in the DFAs of both males and females (Fig. 2), accompanied by differences in coat color patterns and a unique combination of discrete characters and supported by geographic structure.

My findings regarding the morphological and geographic components of the variation in the *L. lugens* complex, concomitantly support the hypotheses of: 1) differentiated natural groups separated by geographic and ecological barriers; and 2) the potential presence of a contact zone between highland and lowland *L. lugens* populations, as a plausible explanation for the three *L. lugens* coat-color variants previously reported in this taxon by Fooden (1963). Based on this evidence, I recognize three geographic variants, two of them introduced as new subspecies of *L. lugens.*

Family Atelidae Gray, 1825
Subfamily Atelinae Gray, 1825
Genus *Lagothrix* É. Geoffroy Saint-Hilaire, 1812

Lagothrix lugens sapiens subsp. nov.
Lagothrix lagothricha lugens of Fooden (1963)
Lagothrix lugens of Groves (2001)

Holotype: Male specimen preserved as a skin and skull in excellent condition, FMNH 70601 (Figs. 5 and 6, skull and skin), collected by Philip Hershkovitz on March 18, 1952, collector number 6146. Measurements of the holotype are included in Table 3.

Type locality: Rio Consaya, Caquetá, Colombia (0°31'59.8"N, 75°6'W, 100 m above sea level).

Type series: The type series includes five specimens, three males and two females preserved as skins and skulls, collected at the same locality and deposited in the Field Museum of Natural History, Chicago, Illinois (FMNH), identified by catalogue numbers FMNH 70602-03 ♂, FMNH 70604-05 ♀.

Diagnosis and Comparison: *Lagothrix lugens sapiens* is characterized by a smaller body and longer tail (average ratio body/tail: 0.68 ♂ n = 3; 0.62 ♀ n = 2) compared to *L. lugens* from the highlands of the Central Cordillera (0.84 ♂ n = 6; 0.77 ♀ n = 6) and *L. lugens* from the piedmonts of the eastern versant of the Colombian Andes (0.84 ♂ n = 9; 0.70 ♀ n = 6). *Lagothrix l. sapiens* can be easily identified by its paler overall coloration, gray to silver-gray trunk and darker limbs and head. It is also characterized by a blackish cap ornamented with a mid-sagittal gray or silver coronal stripe; contrasting with the overall darker coloration and a less noticeable to absent cap in typical *L. lugens* from the piedmonts of the eastern versant of the Andean system (Fig. 6). *Lagothrix l. sapiens* has shorter hair than *L. l. lugens*, particularly at the base of the tail, chest and forearms. Skulls of *L. l. sapiens* are larger than those of *L. lugens* from the highlands of the Central Cordillera, and they are within the range of *L. lugens* from the eastern piedmonts. However, skulls of *L. l. sapiens* average larger than *L. lugens* from the eastern versant of the Andes for 13 of the craniodental measurements analyzed in this work (Table 1). Mandibles of *L. l. sapiens* are larger than those of woolly monkeys from the highlands, but smaller in all measurements compared to those of woolly monkeys from the eastern piedmonts (Table 3).

Description: *External characters* – Large body (458.7 mm ♂ n = 3; 437.5 mm ♀ n = 2) and long tail (660.76 mm ♂ n = 3; 697 mm ♀ n = 2; measurements reported by Fooden 1963), general gray to silver-gray trunk; presence of contrasting darker head characterized by a blackish cap ornamented by a mid-sagittal gray or silver coronal stripe. The tail in *L. l. sapiens* is unicolored, gray to silver-gray not noticeably wider at the base. In *L. l. sapiens*, the arms and the limbs are of the same color as the trunk, silver-gray to dark-gray, with a darker coloration, dark-gray to blackish-gray on the forearms and hands. Ventrally, long hairs on the chest, varying in color from silver gray to brown to blackish brown (Ridgeway 1912). *Skull characters* – Large skull (GSL >110 mm in males and 105 mm in females), elongated caudally; orbits enlarged; massive supraorbital arches, particularly in males; zygomatic width surpassing orbital width from a rostral view; and enlarged choanas.

Distribution: *Lagothrix l. sapiens* seems to be restricted to the lowlands of the eastern versant of Colombia's Eastern Cordillera, between the ríos Caquetá and Caguán, in a region which is

Table 3. Measurements of 28 craniodental variables in individuals of the type series of *Lagothrix lugens sapiens* and *L. lugens defleri*; holotypes.

	L. l. sapiens **FMNH 70601 ♂**	***L. l. defleri*** **FMNH 87775 ♂**
GLS	114.74	115.09
BCL	87.15	85.42
CB	96.68	95.57
PAL	32.55	38.57
ZYG	73.5	69.74
BCW	61.43	60.29
MB	57.62	57.62
BCH	47.78	48.77
INT-ORB	55.67	51.46
AOC	49.05	45.05
AIM	59.17	56.79
OH	25.25	22.78
MAXNAS	37.88	39.3
MFOR	4.04	3.58
FOR-OVA-R	4.95	6.56
FOR-OVA-L	4.58	5.63
MR	14.3	15.36
PR	10.21	11.32
M1W	6.38	6.54
C-C	30.33	28.3
LTR	31.9	32.61
RTR	31.48	32.55
ML	77.82	76.2
RM	53.58	55.36
MH2	46.92	48.56
Wd1	27.6	30.52
MTR	21.06	21.72
C-C1	19.83	20.92

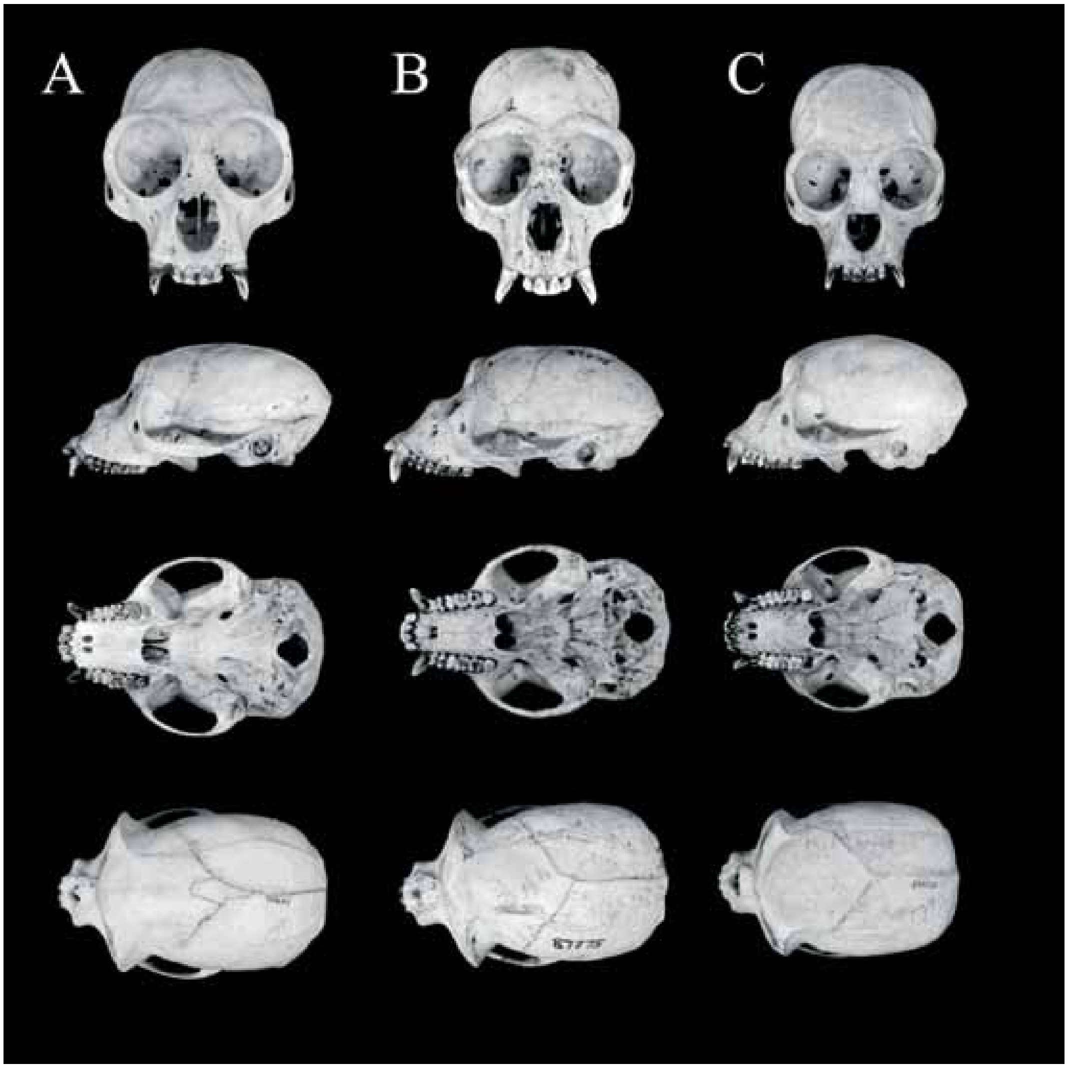

Figure 5. Skulls of holotypes of: A) *Lagothrix lugens sapiens* FMNH 70601 ♂ from Consaya, Caquetá, Colombia; B) *L. l. defleri* FMNH 87775 ♂ collected at Río Yerley, Parque Nacional Natural La Macarena, Meta, Colombia; and a specimen of *L. l. lugens*, FMNH 84550 ♂ collected at Moscopán, Huila.

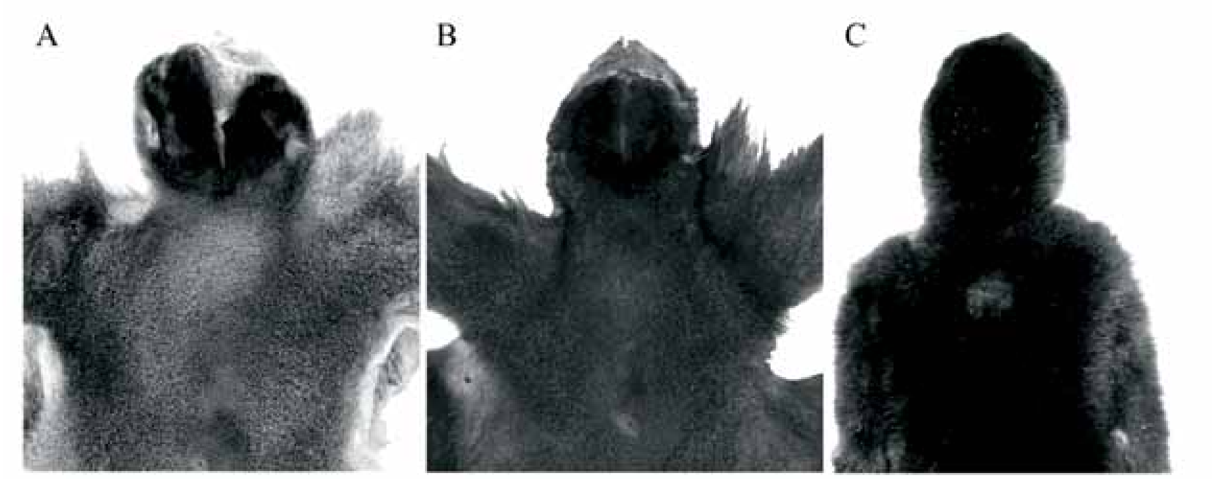

Figure 6. Detail of the upper back of *L. lugens* specimens representing color phases associated with the three skull morphotypes identified in this work and occurring in three contrasting ecosystems: A) FMNH 70601 ♂, from Río Consaya, Caquetá; B) FMNH 87775 ♂, from Río Yerley, Meta; and C) FMNH 84550 ♂, from Moscopán, Huila.

part of the biogeographic district of Caguán, in the Amazonian province (*sensu* Hernández-Camacho *et al.* 1992) (Fig. 7).

Etymology: In his visit to Colombia in 1942, Dr. Philip Hershkovitz established contact with Dr. Jorge Ignácio Hernández-Camacho, the most important figure in Colombian mammalogy in his generation (Patterson 1987). In his phonebook, Dr. Hershkovitz wrote in Spanish "El Sabio" (the wise man) beside Dr. Hernández-Camacho's name. As a double tribute to the life of two remarkable scientists and to celebrate their meeting and all the fruits that this episode brought to the field of Primatology, the author has used the Latin translation of wise (*sapiens*) to designate the newly described taxon. The name *sapiens* highlights as well one the most conspicuous characteristics of the subspecies; its larger skull compared to *L. l. lugens*. The author also gives tribute to the museological endeavors of the FMNH, the institution that housed the specimens used as evidence for the description.

Common name: Woolly monkeys are called "*churucos*" or "*chulucos*" throughout their range in Colombia. I recommend "wise woolly monkey" in English and *churuco sabio* in Spanish.

Lagothrix lugens defleri subsp. nov.
Lagothrix lagothricha lugens of Fooden (1963)
Lagothrix lugens of Groves (2001)

Holotype: Male specimen preserved as a skin and skull in excellent condition, FMNH 87775 (Figs. 5 and 6), collected by Kjell von Sneidern on 24 February, 1957; collector's number 22574.

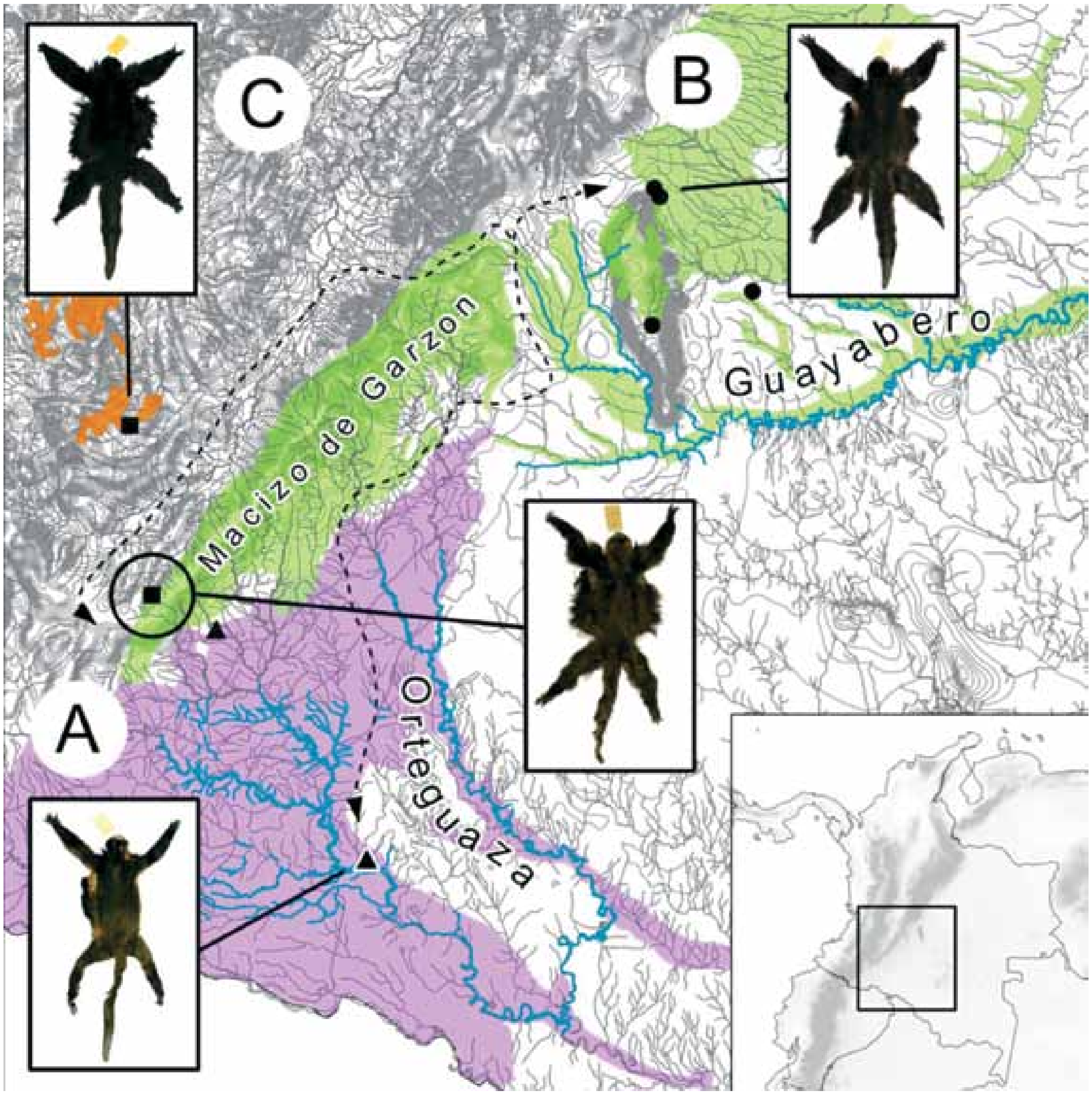

Figure 7. Geologic units associated with *Lagothrix lugens* collecting localities: Amazon Domain (purple), Andean Domain (orange), Guianan Domain (pink), and the Macizo de Garzón Unit (green); *L. l. lugens* (squares), *L. l. sapiens* (triangles); *L. l. defleri* (circles). Encircled square represents the locality of Aguas Claras, Huila, Colombia. Dashed line represents potential routes of gene flow among *L. lugens* populations.

Type locality: Río Yerley, Parque Nacional Natural La Macarena, department of Meta, Colombia (2°53'26.12"N, 75°18'W, 457.2 m [1500 ft] above sea level) (Fig. 7).

Type series: The type series includes four specimens, two males and two females preserved as skins and skulls, also collected with the holotype at Río Yerley FMNH 87776–77 ♂, FMNH 87778–79 ♀.

Diagnosis and Comparisons: *Lagothrix l. defleri* has a larger body than *L. l. lugens* and is within the morphometric range of *L. l. sapiens* in this respect (Table 3), with a shorter tail, broader at the base than in *L. l. sapiens* (see ratios body/tail in previous section). Overall coat color in *L. l. defleri* is darker than that of *L. l. sapiens*, with the hair on the chest and forearms longer than in *L. l. sapiens*. Blackish cap in *L. l. defleri* present, although contrasting less than in *L. l. sapiens*. Internally, skulls of *L. l. defleri* are larger than is typical of *L. l. lugens*; characterized by zygomata not going beyond the orbital width in rostral view, contrasting skulls of *L. l. sapiens* specimens are FMNH 70601 ♂ FMNH 70604-05 ♂; and FMNH 70603 ♀, in which the zygomata goes beyond the orbital width.

Description: Large (535.35 mm ♂ n = 6; 517 mm ♀ n = 6) and long tail (634 mm ♂ n = 6; 669.8 mm ♀ n = 6; measurements reported by Fooden 1963) general dark-gray to brown to brownish black trunk; darker head characterized by a blackish cap ornamented by a mid-sagittal dark gray coronal stripe. *Lagothrix. l. defleri* has a broad tail, particularly at the base, that is blackish-gray to black. In *L. l. defleri*, the arms and the limbs are of the same color as the trunk, dark-gray to brownish-black. Ventrally, long hairs at the chest, varying in color from dark-gray to brown to blackish brown (Ridgeway 1912). The skull of *L. l. defleri* is larger than those of *lugens* and *sapiens* (Table 3), but slender and elongated caudally, and markedly constrained at the anteorbital constriction; orbits are enlarged with massive supraorbital arches in males; zygomatic width smaller than orbital width, particularly noticeable from a rostral view. Mandibles of *L. l. defleri* average larger than adjacent forms.

Distribution: Collecting localities of *L. l. defleri* represent five different biogeographic districts: Piedemonte Casanare-Arauca, and Piedemonte Meta, in the biogeographic province of Orinoquia; Ariari-Guayabero and Macarena in the biogeographic province of La Guayana; and Selvas Nubladas Orientales in the Norandina biogeographic province, as described by Hernández-Camacho *et al.* (1992). The subspecies is thought to occur north of the lower Río Guayabero, where populations formerly identified as *L. lugens* were reported by Klein and Klein (1976), up to the Río Apure at the border between Colombia and Venezuela, based on a record reported by Ruiz-García and Pinedo-Castro (2010) putatively assigned to *L. lugens* (Fig. 7). Most of the specimens of this taxon were collected at the Serranía de la Macarena and the piedmont of the Uribe region (between the Serranía de la Macarena and the Eastern Cordillera).

Etymology: *Lagothrix lugens defleri* is named after Dr. Thomas R. Defler. The innumerable contributions of Dr. Defler to Colombian Primatology are the product of more than 30 years of continuous field work in the Colombian Orinoquia and Amazonia. As part of his efforts in understanding and preserving primate diversity in Colombia, Dr. Defler established the Caparú Biological Field Station (*Caparú* is the Yucuna name for the woolly monkey), dedicated to the training of young Colombian primatologists. As a former student of Dr. Defler at Caparú, I was introduced to field primate studies in 1994; since then, I have enjoyed his friendship and benefitted enormously from his extensive knowledge of primate ecology and evolution.

Common name: Woolly monkeys, genus *Lagothrix* are called "*churucos*" or "c*hulucos*" throughout their distribution in Colombia. I recommend "Defler's woolly monkey" in English and *El churuco de Defler* in Spanish.

A biogeographic hypothesis

The southern range of the Eastern Cordillera of the Colombian Andes, which marks the meeting point of the three identified *L. lugens* geographic variants, constitutes one of the most complex geological units of the country (de Porta 2003). The diverse origin of the parental material in the southern range of the Eastern Cordillera has resulted in the constitution of a mosaic of environments and vegetation types harboring a diverse fauna (Rangel 1997) that potentially promotes the ecological isolation observed among *L. lugens* populations. Genetic data in Ruiz-García and Pinedo-Castro (2010) placed the origin of the genus *Lagothrix* in the early Pleistocene (2.5 Mya), with an early isolation of *L. lugens* populations in the northern Andes of Colombia. The authors hypothesize that the high genetic diversity within this taxon, is explained by genetic drift caused by the fragmentation of suitable highland environments during glacial events (Ruiz-García and Pinedo-Castro 2010). Although the uplift of the Eastern Cordillera is placed around 12 Mya, its most active uplifting has been dated around 2.5 Mya (Adriessen *et al.* 1993; Hoorn 1994; Hoorn *et al.* 1995; Van der Hammen *et al.* 1973), suggesting that the expansion of *L. lugens* into the eastern piedmonts is a relatively recent event. This idea is also reinforced by data in Ruiz-García and Pinedo-Castro (2010) which suggested a recent divergence of the lowland species *L. lagothricha*. In addition, the complex hydrological system associated with the eastern piedmonts of the Andes seems to be an effective physical barrier preventing the dispersion of lowland populations of *L. lugens*. Rivers have been identified as effective barriers isolating natural primate populations and as the primary source of primate diversity (van Roosmalen *et al.* 2002, Hershkovitz 1963, 1979, 1982). A color variant of the titi monkey, genus *Callicebus*, in the northern part of the department of Caquetá, was first identified by Moynihan

(1976), and later formally described as an independent evolutionary lineage, *C. caquetensis*, by Defler *et al.* (2010). Defler *et al.* (2010) described the role of the Río Orteguaza as an effective barrier isolating *C. caquetensis* from closely related taxa north of the Río Guayabero. The newly described taxon *L. l. sapiens,* with its type locality at Consaya, between the ríos Caquetá and Caguán, seems to follow a similar biogeographic pattern, with the Río Caguán isolating this taxon from populations of *L. l. defleri* north of the Río Guayabero.

In summary, I interpret the expansion of *L. lugens* into the piedmonts and lowlands of the eastern versant of the Andes as a recent event, followed by the isolation of lowland populations in pockets characterized by divergent ecological zones and separated by physical barriers such as rivers; a process that has lead to the fixation of different external and internal characters. It is also likely that the geographic limits of divergent populations of *L. lugens*, have been fluctuating as a consequence of glacial and interglacial periods with the eventual genetic intermingle among divergent groups, resulting in hybridization in secondary contact.

Taxonomic note

As mentioned by Defler (2003), when von Humboldt (1812) wrote the holotypic description of Humboldt's woolly monkey, he spelled the species name both *lagotricha* and *lagothricha*. According to some, *lagothricha* (and its variant *lagothrica*) are incorrect Latinizations of the Greek words λἄγο(ς) - lago(s) (hare) + θρἵχο(ς) - thrico(s) (hair) because of the preceding vowel "o," which would require the form "trichos" rather than "thrichos". The use of the two versions was certainly a *lapsus* on von Humboldt's part. When revising the genus, however, Fooden (1963), under Article 24 (24.2) of the International Code of Zoological Nomenclature, chose the variation *lagothricha* as the "correct legal spelling" for *Lagothrix lagothricha*. I followed the determination of precedence of names or acts by the First Reviser. "If two or more names, different or identical, and based on the same or different types, or two or more nomenclatural acts, are published on the same date in the same or different works, the precedence of the names or acts is fixed by the First Reviser unless Article 24.1 applies." (International Commission on Zoological Nomenclature 1999).

Conservation remarks

Lagothrix lugens is the only member of the genus categorized as Critically Endangered (A3cd) on the IUCN Red List, and is considered a high priority for conservation due to population decline (Stevenson and Link 2008). Understanding the causes of the phenotypic variation in *L. lugens* is critical to the implementation of more realistic conservation actions to mitigate the negative effects of both anthropogenic and natural pressures. Two of the herein recognized variants of *L. lugens* are associated with Andean and sub-Andean ecosystems and it is likely that substantial changes in their distributions will take place within the next hundred years due to the predicted effects of global warming on these ecosystems (Urrutia and Vuille 2009). Of particular concern is the situation of *L. lugens lugens* populations from Andean ecosystems (>2,000 m above sea level), which are almost entirely and in many cases completely extirpated from a substantial portion of their natural environments. The piedmonts and lowlands of the eastern versant of the Colombian Andes at the Serranía de la Macarena, habitats of the newly described subspecies, on the other hand, have experienced the devastation of unplanned anthropogenic transformation of forested areas mostly associated with the cultivation of illicit crops (Dávalos and Bejarano 2008). In Colombia, deforestation linked to drug cultivation and transport was likely responsible for more than half the forest loss during the 1990s (Alvarez 2002, 2007). To these risks we have to add the negative effects of petroleum extraction on the piedmonts of the Colombian Andes, and mining occurring across highland ecosystems in Colombia. Urgent measures are required to 1) promote comparative ecological studies among the herein described *L. lugens* variants, and 2) design a conservation plan, which takes into account the taxonomic differentiation proposed in this work.

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Appendix I. Specimens Examined

Lagothrix lugens lugens – COLOMBIA: Huila, Acevedo, FMNH 70574-75♂; FMNH 70577-80♂; FMNH 70581♀; Moscopán FMNH 84550; San Agustín, FMNH 70585♂; 70582-84♀. *Lagothrix lugens sapiens* – COLOMBIA: Caquetá, Río Consaya, FMNH 70601♂; FMNH 70604-05♂; FMNH 70602-03♀. *Lagothrix lugens defleri* – COLOMBIA: Boyacá, Bojabá, FMNH 92331-32♂; FMNH 92333-34♀; Meta, La Macarena FMNH 87775-77♂; FMNH 87781♂; FMNH 87778-79♀.

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Southern Range Extensions for the Critically Endangered Black-and-White Ruffed Lemur *Varecia variegata* and Greater Bamboo Lemur *Prolemur simus*

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Abstract: The Vondrozo-Midongy rainforest corridor in south-eastern Madagascar is an example of a habitat corridor between otherwise disconnected protected areas, and is therefore considered important for the conservation of the endemic biodiversity of the island. Through several years of collaboration with local communities surrounding this corridor, WWF-Madagascar learned that members of some of these communities claimed the existence there of the black-and-white ruffed lemur (*Varecia variegata*) and the greater bamboo lemur (*Prolemur simus*), both regarded as Critically Endangered by the IUCN and not known by the scientific community to be present in the corridor. We therefore surveyed six sites in three communes in May 2010 to confirm this information. We made direct observations of *Varecia variegata* at two sites, which represent a southern extension to the known range of the species. We also found the characteristic feeding remains of *Prolemur simus* in the three most southerly sites, observations which also represent a major southern extension of the known range of this species. However, the feeding signs we found were old, at least a year old by our estimations, so we recommend further research to ascertain whether the population still exists there. The corridor is threatened by many anthropogenic pressures, and further reinforcement of the conservation program for the corridor is therefore likely to be necessary to ensure the viability of endangered lemurs in the region, and the role of the corridor in ensuring biological connectivity between the more substantial forests to the south and north.

Key Words: *Varecia variegata*, *Prolemur simus*, *Hapalemur aureus*, Vondrozo-Midongy corridor, Madagascar, conservation, local knowledge

Introduction

The island of Madagascar, geographically isolated for around 90 million years (Mittermeier *et al.* 2010), is rich in endemic plants and animals (Goodman and Benstead 2003). Various studies have shown that the maintenance of this biological diversity depends on the conservation not only of disconnected protected areas, but also on the habitat corridors that permit biological exchange between them (Burel and Baudry 1999). The southern rainforest corridor between Vondrozo and the Midongy du Sud National Park is one such corridor that is thought to play an important role in the conservation of biodiversity in Madagascar. Within the framework of the project WWF MG0941.01 – *Counting Lemurs – The Biological Corridor Vondrozo-Midongy*, WWF-Madagascar has been collaborating with local communities since 2004 for the conservation of the forest corridor in general, and in particular of lemurs. Members of some of these local communities claim the existence there of the black-and-white ruffed lemur (*Varecia variegata*) and the greater bamboo lemur (*Prolemur simus*) (WWF unpubl. data; Rakotonirina 2006), both Critically Endangered (IUCN 2010) and not known by the scientific community to be present in the corridor. Although having an overall (but patchy) distribution extending through much of the eastern rainforest belt, *V. variegata* is believed not to occur south of the Mananara River (Irwin *et al.* 2005; Mittermeier *et al.* 2008, 2010). *Prolemur simus* is thought to have suffered a major reduction in its distribution since sub-fossil times, and has never been recorded south of the Manampatrana River (Irwin *et al.* 2005; Wright *et al.* 2008; Mittermeier *et al.* 2010), although recent surveys show that it has in fact been largely overlooked in much of its extant range

(Dolch *et al.* 2008; Ravaloharimanitra *et al.* 2011). Our study therefore aimed to confirm the presence of these two species in the corridor, which, if successful, would add considerably to its perceived conservation value, whilst also surveying for other lemur species and identifying threats to the lemur community and their habitat.

Methods

The Vondrozo-Midongy corridor is in the south-east of Madagascar (Fig. 1), and consists principally of low- and mid-altitude rainforest. Annual rainfall ranges from approximately 1,700 mm in the south of the corridor to 2,350 mm in the north. The climate shows marked seasonality, with the heaviest rains between December and March and a drier season from April or May to October (Repoblikan'i Madagascar 2006).

We surveyed six sites in three communes (Table 1); the sites selected based on information gathered previously by WWF project members from local communities regarding the potential presence of *Varecia variegata* or *Prolemur simus*. The commune of Vohimary was surveyed between 5 and 20 May 2010 by Rajaonson and Ratolojanahary, accompanied by Aimé Victor Tombotiana from Centre ValBio. The Bevata and Maliorano communes were surveyed between 2 and 21 May by Rakotonirina and Missirli.

Following courtesy visits to local authorities, we organized meetings with the local community associations responsible for the management of each survey site prior to undertaking the field research. We used these meetings to undertake rapid participatory research to gather local knowledge concerning the lemurs present in their sites and the distribution of bamboo, and to identify threats to the sites. We used photos of locally occurring lemur species to help us, and participatory mapping techniques (Jones *et al.* 2005) to map local features and landmarks. The results of these community meetings helped us identify areas most likely to support *V. variegata*, *P. simus* or other bamboo lemurs *Hapalemur* spp., and accompanied by local guides we then undertook the site visits. At Vohitrambo we made only a brief one-day visit, but we surveyed the other sites for three or four days each (Table 1), for eight to nine hours per day between 06h and 15h along existing trails and in areas of high bamboo density. We recorded the presence of lemurs through direct sightings whenever possible, but also through vocalizations (for *Eulemur* spp.) and feeding signs (for *P. simus* and *Hapalemur* spp.). The feeding signs of *P. simus* on large-stemmed bamboos as described by Dolch *et al.* (2004, 2008) and Ravaloharimanitra *et al.* (2011) are highly distinctive, and members of both survey teams had extensive prior experience in distinguishing between feeding remains of this species, *Hapalemur aureus* and *H. griseus* in Ranomafana National Park and elsewhere, which also allowed us to make approximate estimations of the relative age of the feeding signs. Additionally, we recorded signs of threats, including but not limited to habitat destruction, tree or bamboo cutting, artisanal mining, cattle grazing, and evidence of lemur hunting. We carried out nocturnal surveys at two sites, Marovato and Antanimora. Lemur nomenclature follows Mittermeier *et al.* (2010).

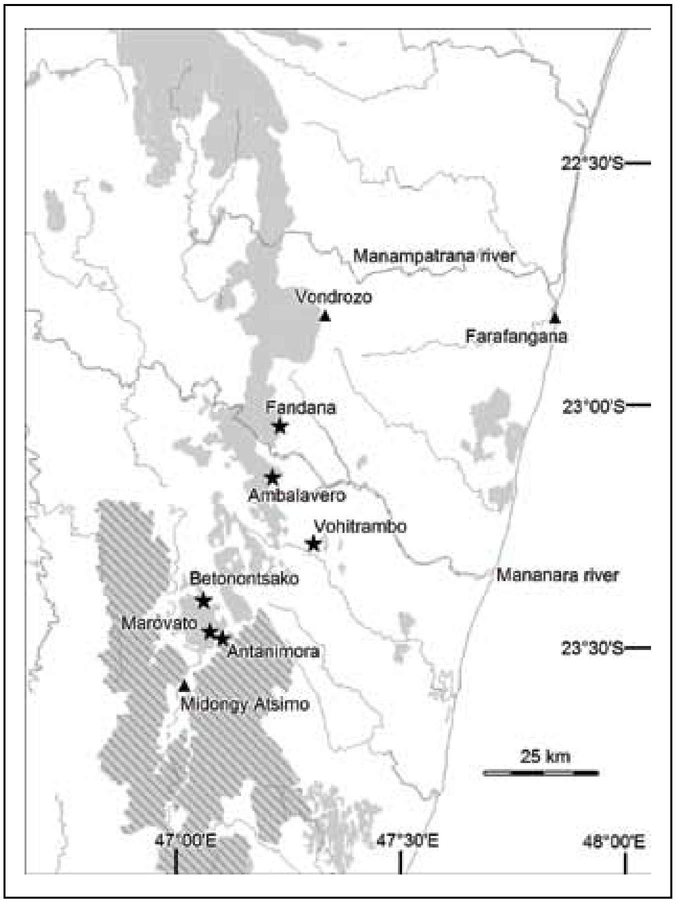

Figure 1. Map showing the location of our survey sites (black stars) in and around the Midongy-Vondrozo Corridor, south-eastern Madagascar, approximate forest cover (light grey), rivers (dark grey), and other selected localities (triangles). The Midongy du Sud National Park is indicated by diagonal lines.

Table 1. The sites surveyed during this study in May 2010, including the name of the local community association (COBA) responsible for their management.

Commune	Site	Latitude	Longitude	Altitude (m)	Survey dates	COBA
Vohimary	Fandana	23°03'S	47°13'E	433–513	17–20 May	Fikambanasoa
Vohimary	Ambalavero	23°09'S	47°12'E	512–578	5–8 May	Manakery
Bevata	Vohitrambo	23°17'S	47°18'E	177	21 May	Bevata
Maliorano	Betonontsako	23°24'S	47°03'E	678–771	13–16 May	Mahabe
Maliorano	Marovato	23°28'S	47°04'E	636–788	3–6 May	Marovato
Maliorano	Antanimora	23°29'S	47°06'E	667–810	8–10 May	Ambodisay

Results

We made direct sightings of *Varecia variegata* at two sites (Figs. 2 and 3), in the Vohimary and Bevata communes. We found old feeding signs of *Prolemur simus* at the three sites in the Maliorano commune (Tables 2 and 3), all on a species of large-stemmed bamboo which we cautiously identified as *Cathariostachys* sp. We also found fresh feeding signs at four sites that we believe to be of *Hapalemur aureus*, but in the absence of direct sightings we refer to them as *Hapalemur* cf. *aureus* in Tables 2 and 3. We were unable to distinguish between the feeding signs of *Hapalemur griseus* and *H. meridionalis* during the survey, neither was our single direct sighting sufficient to separate them, so we have combined our observations of these species in Table 2. We recorded an additional four species by our own direct or indirect observations, and two more, *Lepilemur* sp. and *Daubentonia madagascariensis*, based on local knowledge (Table 2).

Discussion

Varecia variegata

We found *Varecia variegata* at two of the six sites surveyed, Ambalavero and Vohitrambo. Vohitrambo is outside the remaining forest corridor, and the population of *V. variegata* here may not be naturally-occurring; we understand that a few captive individuals of the species were released by local people here around the year 2000 (L. Razafy Fara, unpubl. data). However, the Ambalavero site is in the remaining forest corridor, with no evidence of former release events. Its presence there suggests that the species may be more widely distributed within the corridor. Indeed, local people at the three southern sites surveyed (Antanimora, Marovato and Betonontsako) claimed that *V. variegata* existed in their region several years ago, although they suggested that they passed through their forests rather than being permanent residents (Rakotonirina 2006).

Figures 2 and 3. *Varecia variegata* at the Ambalavero site, May 2010. Photographs by A. Rajaonson.

Table 2. Lemur species recorded in the Vondrozo-Midongy forest corridor, May 2010.

Commune:	**Vohimary**		**Bevata**	**Maliorano**		
Site:	**Fandana**	**Ambalavero**	**Vohitrambo**	**Betonontsako**	**Marovato**	**Antanimora**
Microcebus sp.		*		*	*	Direct
Cheirogaleus sp.				*	Direct	*
Lepilemur sp.					*	
Hapalemur griseus / meridionalis[1]	Feeding signs	Direct	*	Feeding signs	*	Feeding signs
Hapalemur cf. *aureus*[1]	Feeding signs	Feeding signs		Feeding signs	Feeding signs	
Prolemur simus				Old feeding signs	Old feeding sign	Old feeding sign
Eulemur collaris		Direct		*	Heard	Direct
Varecia variegata		Direct	Direct			
Avahi sp.		*		*	Direct	Direct
Daubentonia madagascariensis						*

[1] See text for further explanation

* present according to local knowledge

Both Ambalavero and Vohitrambo are south of the Mananara River, and therefore represent a southern extension to the known range of the species as given in most recent syntheses (Fig. 4; Irwin *et al.* 2005; Wilmé *et al.* 2006; Mittermeier *et al.* 2008, 2010). However, Vasey and Tattersall (2002, illustrated in their Fig. 2) also give a record just south of the Mananara River which appears to have been overlooked by subsequent authors. This observation was made in 1995 close to our observation in Vohitrambo (I. Tattersall, in litt.), suggesting that the species may indeed be naturally-occurring in this area, or perhaps conversely that the release event we refer to above in fact occurred prior to 1995.

Our photos of the animals observed at the Ambalavero site (Figs. 2 and 3) show that the black coloration of the shoulders and upper back is not continuous behind the neck, but is separated by a thick white longitudinal band, a pelage feature considered characteristic of the subspecies *V. variegata variegata* (Mittermeier *et al.* 2010, pp.455 and 464) although apparently also observed within the documented variation of *V. variegata editorum* (Mittermeier *et al.* 2010, pp.458 and 461), which Mittermeier *et al.* (2010) suggest in their distribution maps and English names to be the southern subspecies. However, these authors recognize in their text that the definition and distribution of *Varecia* subspecies is not clear and may require revision. Indeed, Vasey and Tattersall (2002) suggest that the majority (but not all) of records from the south of the species range are of the *V. v. variegata* coloration, including from the most southerly sites on both sides of the Mananara River, an observation consistent with our observations at Ambalavero. We therefore reiterate the recommendation of Mittermeier *et al.* (2008) that a study of the distribution and taxonomy of *Varecia variegata* should be considered a high conservation priority, and we suggest that such a study includes the newly discovered sites we report here.

Prolemur simus

We found the characteristic feeding remains of *Prolemur simus* in the three most southerly sites surveyed, in the commune of Maliorano. These observations represent a major southern extension of the known range of this species, which was not previously known south of the Manampatrana River (Fig. 5; Irwin *et al.* 2005; Wright *et al.* 2008; Mittermeier *et al.* 2010). The sites are located over 110 km south of the previously-known most southerly sites near Karianga (Wright *et al.* 2008), and approximately 90 km south of the Manampatrana River, near which some potential but unconfirmed sites for the species were reported by Rajaonson *et al.* (2010). This southern range extension follows a recent northern range extension reported by Ravaloharimanitra *et al.* (2011), and illustrates again the advantages of surveying for this species through a combination of gathering local knowledge and searching for feeding signs on large-stemmed bamboos (King

Table 3. Details of observations of *Varecia variegata*, *Prolemur simus* and *Hapalemur* cf. *aureus*[1] made within the Vondrozo-Midongy forest corridor, May 2010.

Site	Comments	Latitude	Longitude	Altitude (m)
Varecia variegata				
Ambalavero	Heard	23°09'24.3"S	47°12'35.5"E	572
Ambalavero	Heard	23°09'14.2"S	47°12'24.9"E	565
Ambalavero	Two individuals sighted	23°09'14.6"S	47°12'33.7"E	564
Ambalavero	Four individuals sighted	23°09'15.4"S	47°12'32.3"E	531
Vohitrambo	Direct sighting	23˚17'21.6"S	47˚18'03.3"E	177
Prolemur simus				
Marovato	Old feeding sign	23˚28'24.4"S	47˚04'01.7"E	699
Antanimora	Old feeding sign	23˚29'46.2"S	47˚05'48.4"E	810
Betonontsako	Old feeding sign	23˚24'34.6"S	47˚03'27.6"E	697
Betonontsako	Old feeding sign	23˚24'25.7"S	47˚03'24.8"E	689
Betonontsako	Old feeding sign	23˚24'17.8"S	47˚03'30.1"E	700
Betonontsako	Old feeding sign	23˚24'40.8"S	47˚03'07.7"E	697
Hapalemur cf. *aureus*[1]				
Ambalavero	Fresh feeding sign	23°09'08.0"S	47°12'22.2"E	546
Ambalavero	Fresh feeding sign	23°09'11.4"S	47°12'40.8"E	526
Fandana	Fresh feeding sign	23°03'01.3"S	47°13'26.3"E	513
Fandana	Fresh feeding sign	23°02'45.7"S	47°13'28.3"E	433
Betonontsako	Fresh feeding sign	23˚24'34.6"S	47˚03'27.6"E	697
Betonontsako	Fresh feeding sign	23˚24'33.2"S	47˚03'19.3"E	689
Betonontsako	Fresh feeding sign	23˚24'35.1"S	47˚03'15.1"E	690
Betonontsako	Fresh feeding sign	23˚24'34.8"S	47˚03'13.1"E	705
Betonontsako	Fresh feeding sign	23˚24'38.6"S	47˚03'08.0"E	771
Betonontsako	Fresh feeding sign	23˚24'38.7"S	47˚03'03.8"E	764

[1] See text for further explanation

and Chamberlan 2010; Ravaloharimanitra *et al.* 2011). However, the feeding signs we found were old, at least a year old by our estimations, and at two sites (Marovato and Antanimora) we found only a single feeding sign, compared to four feeding signs at Betonontsako. We therefore recommend further research at this latter site, which supports a high density of giant bamboo, to ascertain whether the population still exists here.

Other species

At four of the survey sites we found fresh feeding signs that we believe to be of *Hapalemur aureus*. Two of us (Rakotonirina and Rajaonson) have extensive experience of differentiating the feeding signs of *H. aureus* and *H. griseus* in the region of Ranomafana National Park, and the signs we found are identical to those of *H. aureus*. If confirmed, these sites represent a major southern range extension for this species (Irwin *et al.* 2005; Mittermeier *et al.* 2008, 2010); however, in the absence of direct sightings, we cannot be absolutely certain of the presence of *H. aureus* at the sites, so we recommend further research for confirmation. We also found feeding signs at four sites, and one direct sighting, that we attributed to *Hapalemur griseus*. However, based on the species distributions proposed by Mittermeier *et al.* (2010), these records may in fact be of *H. meridionalis* at some of the southern sites. It seems unlikely that these species can be reliably separated from feeding remains, and therefore further research is required to ascertain the distribution of these species in the study area. We recorded a further six species during the surveys (some only to generic level), none of which were

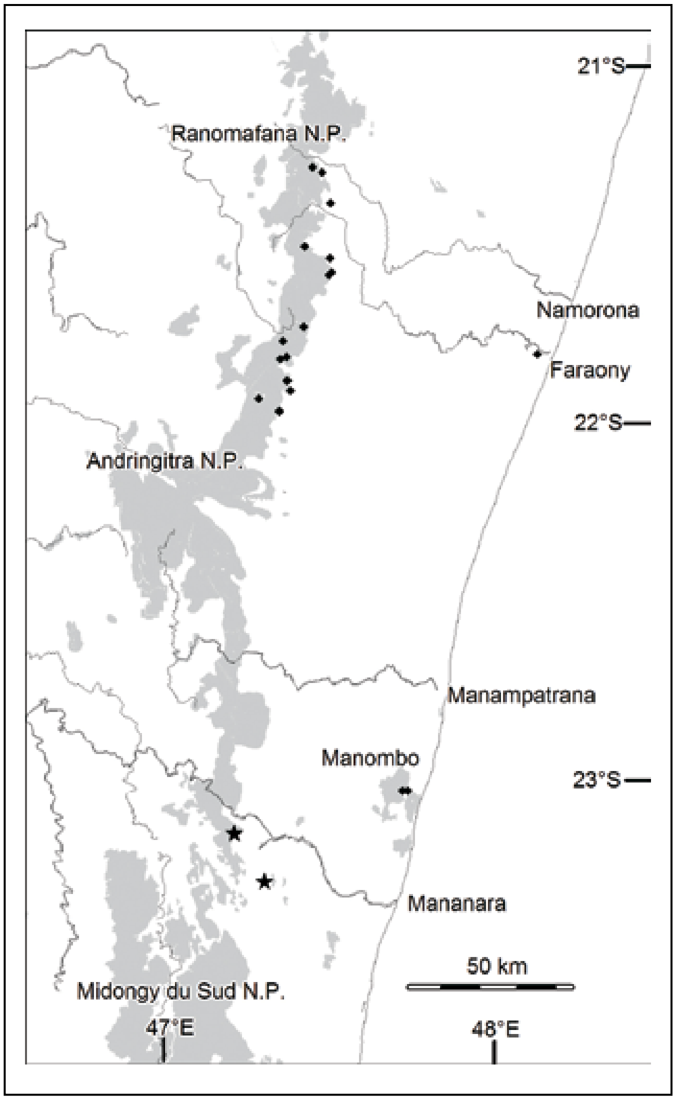

Figure 4. Map showing the *Varecia variegata* sites newly reported here (black stars), sites previously known to support *V. variegata* in south-eastern Madagascar (diamonds), approximate forest cover (light grey), major rivers (dark grey, with names), and other selected localities (named; NP = National Park). Locations of previous *V. variegata* sites are taken primarily from Wilmé *et al.* (2006), with additional sites from Deppe *et al.* (2007), Delmore *et al.* (2009) and Rajaonson *et al.* (2010).

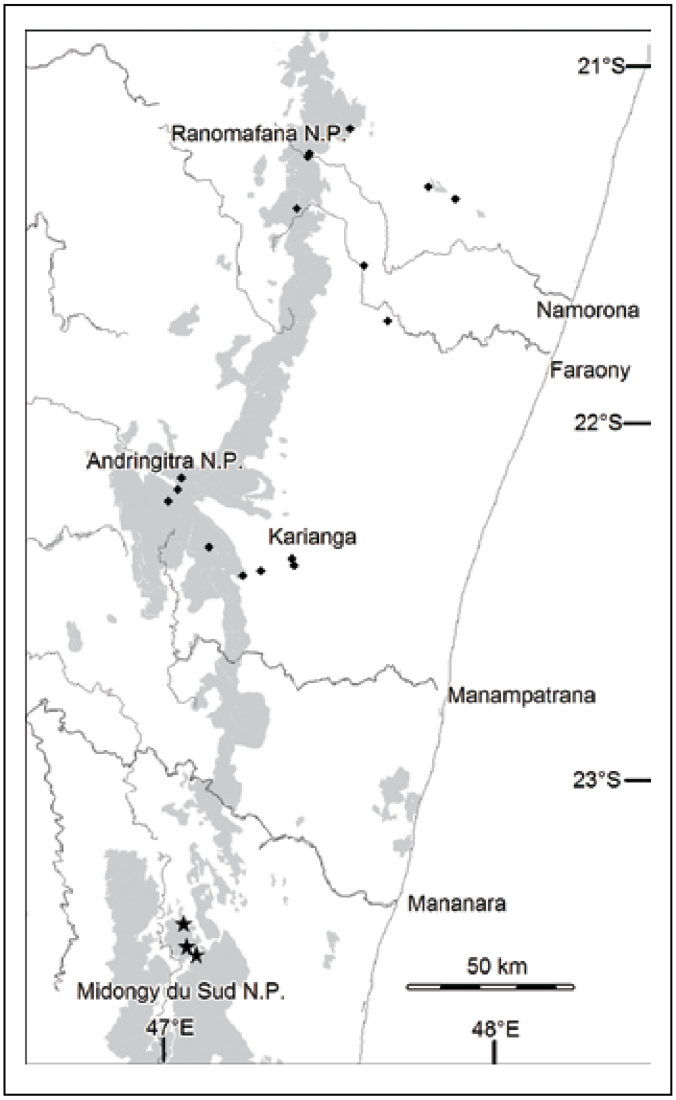

Figure 5. Map showing the *Prolemur simus* sites newly reported here (black stars), sites previously known to support *P. simus* in south-eastern Madagascar (diamonds), approximate forest cover (light grey), major rivers (dark grey, with names), and other selected localities (named; NP = National Park). Locations of previous *P. simus* sites are taken primarily from Wright *et al.* (2008), with additional sites from Meier and Rumpler (1987), Andriaholinirina *et al.* (2003), Delmore *et al.* (2009) and Rajaonson *et al.* (2010).

unexpected based on current knowledge of species distributions as given by Mittermeier *et al.* (2010). The level of local knowledge concerning the presence of lemur species varied greatly between sites, and coupled with the relatively rapid nature of our surveys we almost certainly overlooked some species at each site.

Threats and conservation

Our confirmation of the presence of *Varecia variegata* and *Prolemur simus* in the Vondrozo-Midongy corridor, both listed as Critically Endangered by IUCN (2010), illustrates the high conservation value of the area, and will hopefully stimulate increased awareness at a national and international level of the associated conservation challenges. The corridor is clearly threatened by many anthropogenic pressures. Long-term deforestation has resulted in the corridor currently existing as a very narrow strip of forest which is becoming increasingly fragmented and disturbed. WWF-Madagascar has been working with local populations surrounding the corridor since 2000 in the north, and since 2004 in the south, to ensure biological connectivity in the region. Many local community associations have been created since 2005, with the goal of transferring management responsibility of forest patches from regional government to the local communities themselves (WWF-Madagascar, unpubl. reports). In the Maliorano Commune, the three community associations responsible for the three sites we visited appeared to be well aware of the importance of biodiversity conservation in general, and of lemurs in particular. We found no evidence of lemur hunting in these three sites, which contrasts with the situation we found in the same area in 2006 when lemur hunting was common (Rakotonirina 2006). The cutting of trees for local use in these three sites also appeared to be less frequent than in 2006. However, forest disturbance remains a threat, cattle grazing and cutting of bamboos is still apparent, and local populations remain poor despite the development of various alternative economic opportunities through the WWF program.

At the more northerly survey sites, in the Commune of Vohimary, the forests we visited are generally smaller and more fragmented due to encroaching slash-and-burn agriculture, and the remaining forest areas are highly degraded. Artisanal mining is a principal cause of this degradation, and appears to have become the major source of income for the local populations. In addition, the Ambalavero site is being used as a route for trade in tobacco and locally-produced rum.

Considering these diverse pressures on a corridor already diminished in forest cover, the viability of the remaining lemur populations must surely be questioned. Further work is required to determine distributions, densities and viabilities of these populations, particularly of those species considered Critically Endangered such as *Prolemur simus* and *Varecia variegata*. *Prolemur simus* has a specialized diet dominated by large-stemmed bamboos (Tan 1999; Dolch *et al.* 2008; Ravaloharimanitra *et al.* 2011) and can exist in degraded habitats if bamboo is present and other, as yet undetermined, factors permit (Wright *et al.* 2009; Ravaloharimanitra *et al.* 2011). *Varecia variegata*, however, appears to be very sensitive to habitat loss and fragmentation (Vasey 2003), and recent local extinctions of the species have been recorded elsewhere, thought to have been driven by these factors coupled with hunting pressure (Beaucent and Fayolle 2008). Further reinforcement of the conservation program for the corridor is therefore likely to be necessary to ensure the survival of this and other species in the region, and consequently the role of the corridor in ensuring biological connectivity between the more substantial forests to the south and north.

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Human-Chimpanzee Sympatry and Interactions in Cantanhez National Park, Guinea-Bissau: Current Research and Future Directions

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Abstract: Increasing human populations and the rapid conversion of forest to agricultural land increase the likelihood of interactions and conflict between humans and nonhuman primates. Understanding such interactions requires a broad cross-disciplinary approach that assesses the implications of sympatry for primate conservation and human social, cultural and economic needs. Although chimpanzees were declared extinct in Guinea-Bissau in 1988, recent reports estimate that between 600 and 1,000 individuals are currently present, with the largest population occupying the Cantanhez National Park (105,700 ha; northeast limit: 11°22'58"N,14°46'12"W; southwest limit: 11°2'18"N,15°15'58"W). These heavily fragmented coastal forests have been identified as one of seven priority areas in West Africa for urgent chimpanzee conservation efforts (Kormos *et al.* 2003. *West African Chimpanzees. Status Survey and Conservation Action Plan*. IUCN, Gland. 2003). Here we set the context for human-chimpanzee sympatry in Guinea-Bissau, and provide a platform from which further studies can expand. We review past findings that might affect current and future sympatric relationships, and integrate preliminary data on resource competition from one hitherto unstudied chimpanzee (*Pan troglodytes verus*) community inhabiting a forested-agricultural matrix in Caiquene and Cadique, central Cantanhez National Park. While local human cultural traditions provide a degree of tolerance and protection to chimpanzees in Cantanhez National Park, which is beneficial for long-term conservation initiatives, human-chimpanzee interactions have the potential to grow increasingly negative in character, especially as human populations expand and further pressure is exerted on the land.

Key words: Human-chimpanzee interactions; conflict; resource competition; Guinea-Bissau

Introduction

Increasing human populations and the rapid conversion of forest to agricultural land mostly have a negative impact on nonhuman primates (hereafter primates) by reducing and isolating ranging areas and increasing the likelihood of spatial and ecological overlap. In certain situations traditional protection towards primates, through folklore or religious practices, as well as more recent conservation initiatives has meant that some species inhabit increasingly human-influenced environments in exceptional proximity to people (Fuentes and Wolfe 2002; Paterson and Wallis 2005). The nature of human-primate interactions varies but is often characterized by resource competition, for example over crops and wild resources, and increasing conflict (Kinnaird 1992; Hill 2005). A broad cross-disciplinary approach, such as that used in ethnoprimatological research, increases our understanding of the realities facing both humans and primates and the sustainability of their relationships (see Fuentes and Wolfe 2002 and Fuentes and Hockings 2010 for overviews).

Human-primate conflict is a critical issue when it threatens the economic and social security of rural people as well as compromising biodiversity conservation initiatives (Naughton-Treves 1997). Conflict levels are likely influenced by people's 'capacity' to tolerate problematic wildlife behaviors such as crop-raiding. This is linked to various socio-economic factors such as the commercial value of a crop type, and might also be linked to aspects of development (Hill and Webber 2010). There are, however, important aspects concerning attitude that influence human conceptualizations of conflict (Lee and Priston 2005; Naughton-Treves and Treves 2005). People base their perceptions and attitudes of primates not only upon facts and experiences, but also upon numerous social factors such as cultural norms, expectations, folklore and beliefs (Hill *et al.* 2002; Saj *et al.* 2006; Dickman 2010). In protected areas, where people are legally inhibited from employing traditional methods of dealing with problem wildlife such as hunting, competition over cultivated resources can easily escalate (Madden 2004; Webber *et al.* 2007).

Effective mitigation strategies are urgently required in order to resolve human-primate conflicts (Hockings and Humle 2009). Such measures are either indirect, through increasing tolerance of wildlife using techniques such as environmental education, or direct, by reducing the frequency of human-wildlife interactions and severity of wildlife damage, through land-use planning, for example (Hockings and McLennan under review). It is clear that a detailed understanding of the issues surrounding a potential conflict situation is the first step towards reconciling conflict between humans and primates (Woodroffe *et al.* 2005).

Chimpanzees in anthropogenic habitats

Chimpanzees (*Pan troglodytes*) in particular are of special importance in terms of their complex social and cultural relationship with humans, and are often attributed human-like characteristics (Kohler 2005). Likewise, they are widely used by conservation organizations as a charismatic umbrella species for conservation. Although chimpanzees are considered ripe fruit specialists (Goodall 1986; Wrangham *et al.* 1998), they show high levels of ecological and behavioral flexibility and are able to adapt to areas of secondary vegetation and human agriculture impinging on their natural habitat (Reynolds 2005; Yamakoshi 2011). They frequently conflict with the interests of local people, however, due to crop-raiding, and in some cases, by threatening people's personal safety (McLennan 2008; Hockings *et al.* 2009, 2010). In reality chimpanzees are particularly vulnerable to local extinction due to their now highly restricted ranges (many outside of protected areas), slow life history, and large body mass, and are extremely susceptible to a range of anthropogenic activities, including deforestation, agricultural expansion and hunting (Kormos *et al.* 2003).

Using a cross-disciplinary perspective, we here describe the context for human-chimpanzee sympatry and interactions in Guinea Bissau, and indicate directions for further studies. In particular, we review historical aspects relevant to our understanding of current relationships and integrate new data from one hitherto unstudied chimpanzee (*Pan troglodytes verus*) community inhabiting a forested-agricultural matrix in Caiquene and Cadique-Nalu (hereafter Cadique),central Cantanhez National Park. We conclude by discussing the conservation management of these apes and the potential for long-term coexistence in changing habitats.

Human-influenced habitat in Guinea-Bissau

The Republic of Guinea-Bissau lies on Africa's north-western coast and covers an area of 13,948 km². The continental part of Guinea-Bissau can be divided into three regions: coastal lowlands, the interior plain, and the north-eastern highlands. Cantanhez National Park (CNP) is in the south-western part of Guinea-Bissau, in the Tombali Administrative Region (see Fig. 1; northeast limit: 11°22'58"N, 14°46'12"W; southwest limit: 11°2'18"N, 15°15'58"W). Cantanhez was declared a National Park by presidential decree in 2008 and

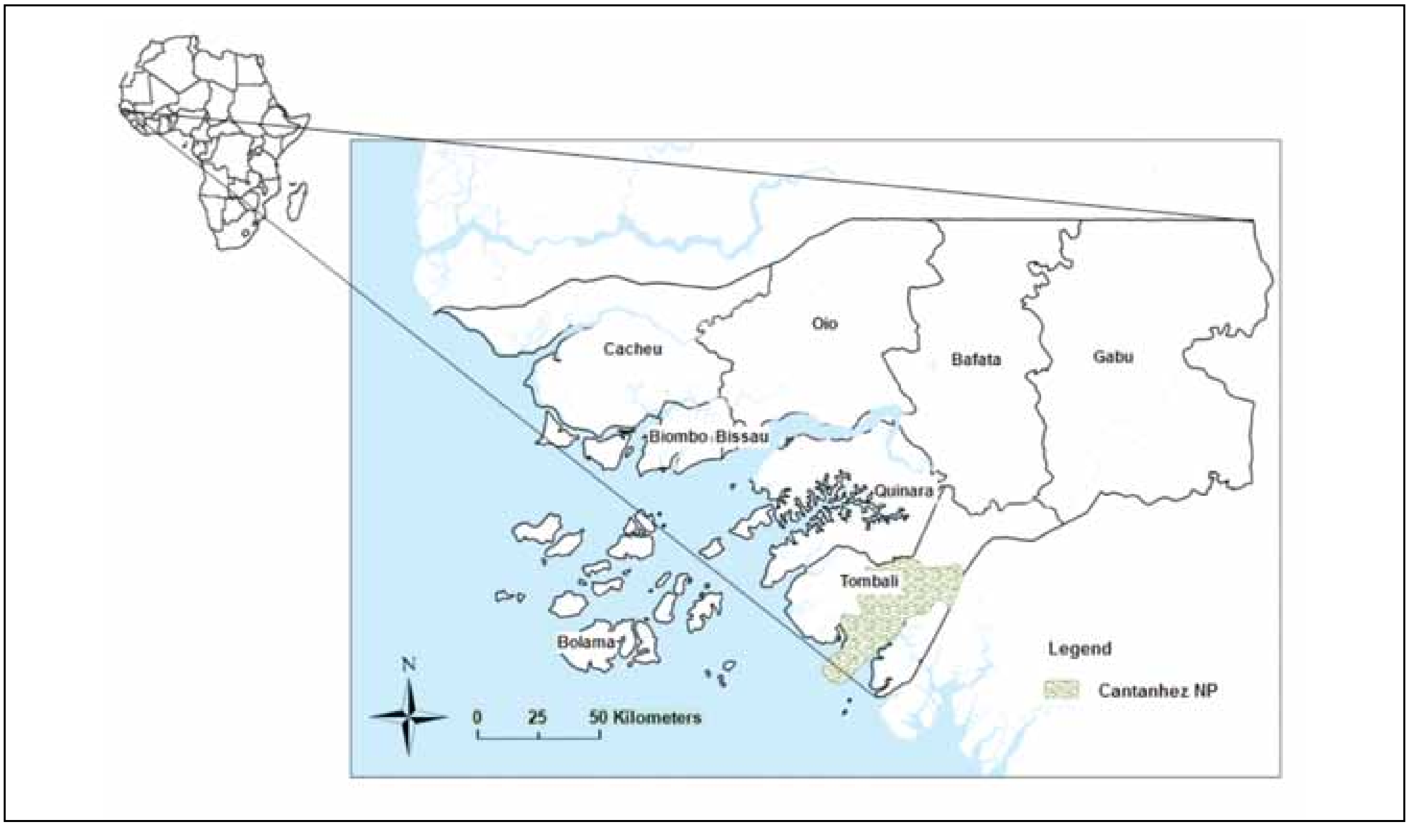

Figure 1. Location of Guinea-Bissau in west Africa and Cantanhez National Park in Tombali, Guinea-Bissau.

following a general agreement between the central and local authorities and the local population for the need to take action to conserve the biodiversity of this area, in addition to the promise of income-generating schemes associated with ecotourism (Gippoliti *et al.* 2003).

Due to seasonal patterns of the intertropical convergence zone, rainfall in Guinea-Bissau is bimodal: there is a long dry season from November to May and a rainy season from June to October (Catarino 2004). An average of 1400–2500 mm of rain falls per year and temperatures are at their lowest in January (24.7°C) and their highest in July (28.0°C) (Gippoliti *et al.* 2003). CNP has a mosaic environment of forests, savanna and mangroves (Gippoliti and Dell'Omo 2003; Catarino 2004), and supports a large proportion of the country's remaining closed (or primary subhumid) forest (Oom *et al.* 2009). The World Wide Fund for Nature (WWF) has identified the Cantanhez Forest as one of the 200 most important ecoregions in the world, being as it is one of the last remaining fragments of humid forest in West Africa. These heavily fragmented coastal forests have been identified as one of seven priority areas in West Africa for chimpanzee conservation efforts (Kormos *et al.* 2003). Even though forests in Cantanhez have been officially classified as protected and as non-hunting reserves, the regulations are not enforced, and there is very little formal protection for the forests and wildlife there.

Human activities have resulted in areas of scrubland and cultivation, with roads and paths dissecting the national park. Using satellite imagery, Oom *et al.* (2009) identified a marked trend in forest degradation in Tombali from 1990–2007 (prior to the establishment of CNP), with a transition from closed to open forest and savanna-woodland. This loss of closed forest has been due to forest cutting for swidden (or 'slash-and-burn') agriculture for subsistence crops such as rice (*Oryza* spp.), cassava (*Manihot esculenta*) and beans (*Vigna unguiculata*), and the conversion of forest into cashew (*Anacardium occidentalis*) plantations. The proportion of dry land used for food production is continually increasing in CNP due to increasing numbers of people, many unfamiliar with more traditional coastal rice farming practices in mudflats or '*bolanha*' areas. Many are opting to grow cashew instead of cultivating rice in these difficult-to-farm areas.

Guinea-Bissau is the sixth largest exporter of unprocessed cashew nuts and many farmers now depend on the crop for cash income (Barry *et al.* 2007). Most of the cashews exported are grown and collected by small, rural farmers and their families (90,000 households), rather than large commercial growers (2,200 '*ponteiros*') whose large plantations cover less than 27% of the country's arable land. Forested and arable land is being converted for cashew production at a rate of approximately 4% per year (taken from Barry *et al.* 2007). Cashew orchards are abundant in CNP, and cashew trees are often planted following the cultivation of other subsistence crops. Cashew farming is less labor intensive than rice farming, and the earnings from cashew nuts are often used by local people to buy imported rice (Barry *et al.* 2007).

Biological and anthropogenic diversity

There are numerous ethnic groups in Guinea-Bissau, including Balanta (30%), Fula (20%), Manjaco (14%), Mandinga (13%), and Papel (7%) (Sousa and Frazão-Moreira 2010). The Nalu people are believed to have settled in the Cantanhez area by at least the 15th Century and are the last remaining 'traditional owners of the land' (Baran and Tous 2000). A number of different ethnic groups have entered the area since then, the most important of which are the Balanta, the Fula (who introduced the Islamic religion) and the Sosso (Carvalho 1949; Temudo and Schiefer 2003). About 70% of the population lives in rural areas (with an urbanization rate of approximately 3.2%), and the livelihoods of the majority depend on agriculture (CIA 2010). There are 110 villages (locally known as *tabancas*) in the 105,700-ha CNP, and a recent population census estimates 22,505 people living there, with a population density of approximately 20 people/km².

The wildlife of the CNP is very rich and includes seven primates (Gippoliti and Dell'Omo 1996); the western chimpanzee, colobus monkeys (*Procolobus badius temminckii* and *Colobus polykomos*), Guinea baboon (*Papio papio*), green monkey (*Chlorocebus aethiops sabaeus*), Campbell's monkey (*Cercopithecus campbelli*) and Senegal bushbaby (*Galago senegalensis*). Controlled seasonal hunting in the national park is permitted by law, but only by local people and for certain game species such as warthog (*Phacochoerus africanus africanus*) and duiker (*Cephalophus* spp.). Primates are officially fully protected there, but they are still illegally hunted for meat; mostly colobus and baboons. The young of certain species, mostly baboons, are often captured to keep as pets.

Chimpanzee conservation in Guinea-Bissau

Of the four recognized subspecies of chimpanzees, the western chimpanzee is the second most-threatened. It has been extirpated from at least two countries, and is on the verge of extinction in five others (Kormos *et al.* 2003). Chimpanzees are classified as Endangered on the IUCN Red List (IUCN 2008), and are thus legally protected in Guinea-Bissau. Although chimpanzees were declared extinct there in 1988 (Lee *et al.* 1988; Teleki 1989; Butynski 2001), subsequent reports estimated that between 600 and 1,000 individuals are currently present (Gippoliti *et al.* 2003). More recently, Torres *et al.* (2010) have shown that suitable forest habitats in CNP (also includes parts of the Cacine and Catio regions) decreased by approximately 11% (270 km²) from 1986 to 2003 and, depending on three different chimpanzee density estimates, this will have resulted in a decrease of between 157 and 1103 individuals. Using the lowest density estimate of 0.5 individuals/km², the current (2003) population of chimpanzees in CNP is predicted to be fewer than 400 individuals. Based on behavioral observations (sightings, vocalizations, road-crossing points) of chimpanzees, the location of chimpanzee sign (nests, feces, knuckle prints, feeding remains), local reports and natural and man-made barriers, we have estimated that several different chimpanzee communities are present in the forested areas of central Cantanhez (see Fig. 2; Hockings unpublished data); this is supported by preliminary genetic analyses (Rui Sá unpublished data). Using questionnaire data collected from local hunters, Brugière *et al.* (2009) suggested that chimpanzees are also present around all surveyed villages (n = 70) in southern Guinea-Bissau, more specifically between the Corubal River and the border with Guinea.

Human-chimpanzee interactions in Guinea-Bissau

Like other sites in Africa (for example, Bossou, Guinea: Hockings *et al.* 2006, 2009; Bulindi, Uganda: McLennan 2008), local people in Guinea-Bissau frequently come into contact with chimpanzees on roads, in cultivated areas, and around the edges of forest fragments. Although detailed data on human-chimpanzee interactions in Guinea-Bissau are lacking, interactions can be broadly categorized into several non-mutually exclusive areas, including disease transmission, cultural attitudes/perceptions towards chimpanzees and their habitat, and overlapping cultivated and wild resource use.

Disease transmission

Data on disease transmission between local people and chimpanzees in Guinea-Bissau are only now becoming available. Humans and chimpanzees in Cantanhez share various parasites, in particular *Blastocystis hominis* and *Trichuris trichura*, the prevalence of which indicates that degree of habitat disturbance might affect transmission and persistence of such pathogens in this area (Sá *et al.* 2009). The potential for bi-directional pathogen exchange (for example, Engel *et al.* 2002), its relationship with range overlap between humans and primates, and its effect on primate conservation in Guinea-Bissau certainly requires detailed research. Furthermore, the risk of disease transmission between researchers and chimpanzees (as documented by Köndgen *et al.* 2008 for chimpanzees at Taï National Park, Côte d'Ivoire) must be properly considered when deciding whether to habituate ape populations in Cantanhez for scientific research or tourism.

Local cultural attitudes

Cultural attitudes towards flora and fauna by some ethnic groups, including the Nalu, are also an important component of interaction, with certain forests and tree species (including *Ceiba pentandra*, *Parinari excelsa*, *Dialium guineense*, and *Treculia africana*) having symbolic and religious meanings that offer a degree of traditional habitat protection (Frazão-Moreira 2001, 2009; Sousa and Frazão-Moreira 2010). Likewise, chimpanzees — *Dári* in Creole — are not hunted for meat in this area due to local taboos (i.e., unwritten rules or prohibitions that regulate human behavior) as they are considered too similar to humans (Gippoliti *et al.* 2003; Brugière *et al.* 2009). In agreement, Costa *et al.* (2008) showed that

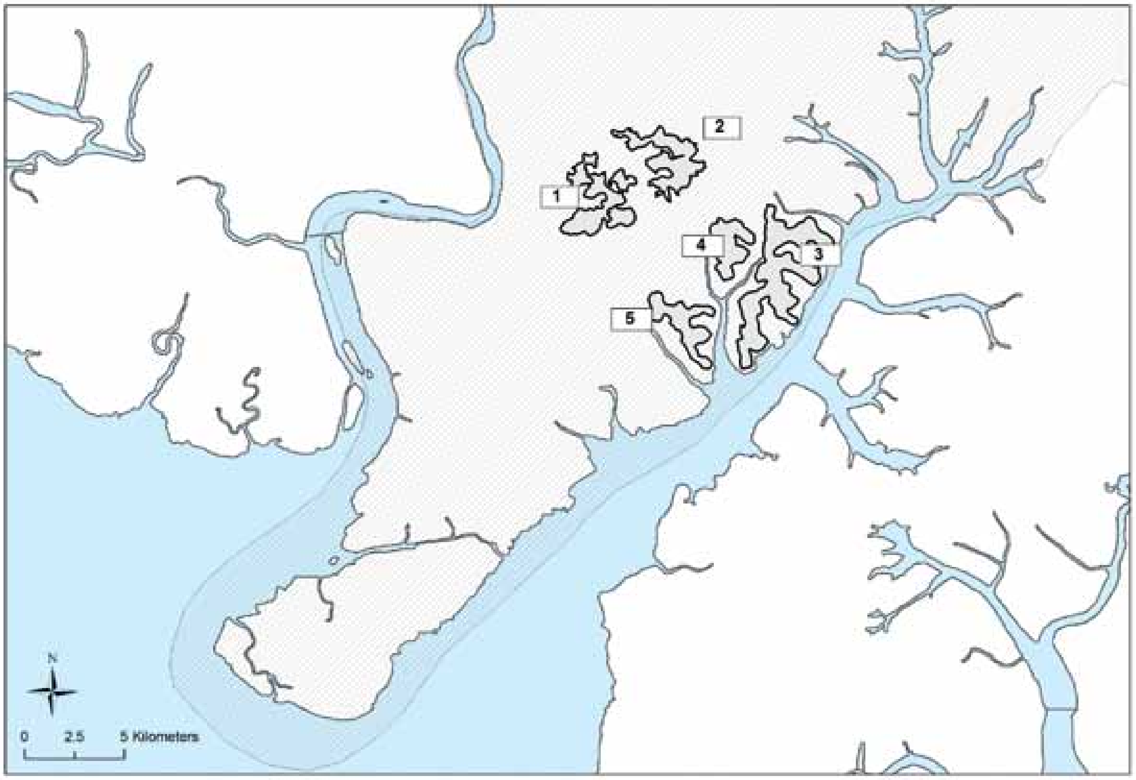

Figure 2. The forests of central Cantanhez National Park containing chimpanzees; (1) Cadique and Caiquene, (2) Lautchande, (3) Camocote and Cambeque, (4) Madina, and (5) Catomboi.

chimpanzees in Cantanhez are classified as 'highly non-edible' among the Balanta ethnic group, owing to their resemblance to humans. Although chimpanzee meat is not consumed, there is some suggestion that other body parts still might be used in traditional medicine (Gippoliti *et al.* 2003), and an illegal pet trade in infant chimpanzees persists (Casanova and Sousa 2006).

A population of chimpanzees living in proximity to the villages of Caiquene and Cadique currently show little evidence of aggressive behaviors towards local people, and informal conversations with villagers suggest that chimpanzees are not considered a physical threat in this particular location (for the opposite situation see Hockings *et al.* 2010; McLennan and Hill 2010). Preliminary observations suggest that people mostly remain calm in the presence of the chimpanzees (Hockings unpublished data; see Fig. 3). To corroborate this, to date there have been no reports of attacks by chimpanzees on local people at this site, and this likely contributes to their indifferent or positive perceptions of chimpanzees in this area.

Overlapping resource use – crops

In terms of resource competition, 89% of interviewees from a questionnaire survey of local hunters in southern Guinea-Bissau reported that chimpanzees raided crops, especially maize (*Zea mays*) and sugarcane (*Saccharum* sp.) (Brugière *et al.* 2009). A range of subsistence foods as well as cash crops are cultivated by people in the villages of Caiquene and Cadique. Most fruit trees are in small patches close to people's houses, and the majority of cultivated areas contain the cash-crop cashew (Hockings and Sousa in press). Chimpanzees in this community eat at least 10 different crop species, including papaya (*Carica papaya*), cashew (*Anacardium occidentale*), cowpea bean (*Vigna unguiculata*), baobab (*Adansonia digitata*), mango (*Mangifera indica*) and orange (*Citrus sinensis*). Chimpanzees at Caiquene-Cadique eat the juicy cashew pseudofruit (hereafter fruit) at numerous locations throughout their home range. The nut is never consumed probably because it is enclosed by a potent skin irritant (Hockings and Sousa in press). The skin of the cashew fruit is fragile, making it less suitable than other fruits for transport and retail. As a result the fruits are rarely sold, and it is acceptable to take fruit from a farm for personal consumption if the nut is left. Farmers report that chimpanzees sometimes damage cashew trees by snapping branches to obtain the fruits more easily, but also point to a benefit of chimpanzee raiding as chimpanzees leave the nuts in manageable piles thereby making nut collection easier (Hockings and Sousa in press).

Figure 3. An adult male chimpanzee in Caiquene-Cadique crossing a road that bisects the chimpanzees' home range.

While the level of conflict over cashew, the country's major cash crop, currently appears quite low in Caiquene and Cadique due to differential use of cashew plants by humans and chimpanzees (Hockings and Sousa in press), the raiding of other crops such as oranges in parts of CNP are known to have resulted in retaliatory killings of chimpanzees by farmers.

Overlapping forest resource use

Local people in CNP use a wide range of forest resources for construction, medicinal and subsistence purposes (see Frazão-Moreira [2009] for a detailed review of resource use by Nalu people). Although it is too early to precisely catalogue the feeding behaviors of chimpanzees in CNP, we mention below some prominent wild foods that both chimpanzees and local people use in Caiquene and Cadique.

There are three species of palm tree in the chimpanzees' known range, namely *Elaeis guineensis* (oil palm), *Borassus aethiopum* (African fan palm) and *Phoenix reclinata* (wild date palm). As elsewhere in West Africa (for example, in Guinea: Humle and Matsuzawa 2004), oil palms are scattered on the edges of the forest (see Sousa *et al.* 2011) and local people harvest the fruits mainly to produce oil. Although chimpanzees eat the fruit, pith and flower (Sousa *et al.* 2011), the abundance of oil palms and their distribution on the edges of forests means that there is very little competition felt by the villagers. The African fan palm is protected, and its use by local people for construction materials is restricted but commonplace. The production of alcohol from this species is forbidden as it ultimately kills the tree, but some local people continue to use it for this purpose. Temudo and Schiefer (2003) suggest that because of this, the palm has almost completely disappeared from the Cantanhez area. Chimpanzees at Caiquene-Cadique eat the fruits of this palm (the fruits are around 500g each and have a large and fibrous pulp), although its importance in their diet is unknown. The wild date palm is found extensively in wetter areas bordering the mangroves. Although human use of this palm appears low, chimpanzees consume the pith and discard distinctive wadges. Consumption of the fruit has not yet been confirmed, but it is seasonally important for chimpanzees living in a forest-farm matrix at Bulindi, Uganda, where its consumption by chimpanzees is negatively related to their crop feeding (McLennan 2010).

Other chimpanzee food species identified include the fruits of *Parinari excelsa* and *Dialium guineense*, which are eaten infrequently by local people (children pick the fruits at the edges of forests and along roads, see Fig. 4), although the timber is used in construction. Chimpanzees at

Figure 4. A child eating wild *Dialium* fruit in a cashew plantation.

Caiquene-Cadique frequently enter cashew plantations to eat fruits from wild shade trees such as *Parkia biglobosa.* Chimpanzees in this area also approach human settlements to raid beehives, and are reported to compete with local people for access to water wells in the dry season (Sousa unpublished data). There is a need for detailed ecological and behavioral investigations into human and chimpanzee plant consumption and extraction rates in CNP, and more widely in Guinea-Bissau. It is important to examine whether any wild foods are exploited by local people for commercial reasons, as occurs for example, at Fongoli in Senegal. Pruetz (2002) found that 17 naturally occurring plant species were eaten by both humans and chimpanzees in the Tomboronkoto region in Senegal. The fruit from the forest liana *Saba senegalensis* is a critical food source for chimpanzees at Fongoli in the dry season, but it also serves as a cash crop for humans during times of hardship. Such information will help to guide effective management in CNP, in an effort to ensure that unsustainable harvesting of wild fruits by humans does not reduce wild fruit availability to such an extent that chimpanzees will be forced to seek alternatives, perhaps increasing consumption of cultivated crops. Likewise, information on the economic importance of wild foods to local humans can be incorporated into sustainable management strategies.

Conclusions

For the most part, chimpanzees inhabiting large protected areas are less likely to interact with people and compete over resources — crops are generally not available in protected areas and the chimpanzees' sizeable home ranges provide sufficient wild food. However, it is evident that chimpanzees in Cantanhez National Park and other parts of Guinea-Bissau are being forced to adapt to human encroachment and use of the forest. An inevitable consequence is a continuing rise in human–chimpanzee interactions, which have the potential to grow increasingly negative in character, especially as human populations increase and further pressure is exerted on the land. Conflict-mitigation strategies that target problematic wildlife behaviors such as crop-raiding are particularly complicated to establish for cognitively complex species, and require a good understanding of the species' behavior. When species have protected status, theoretically problem animals should only be deterred, translocated or tolerated, hence proactive management is required. Continuing research to understand these complex interactions and chimpanzee behavior will guide future land-use plans, for example through restrictive planting of attractive and high-conflict crops in the national park (see Hockings and McLennan under review).

Chimpanzees in Caiquene-Cadique occur at a density of approximately 3 individuals/km^2, classified as high density by Torres *et al.* (2010). This corroborates findings elsewhere that chimpanzee populations can persist in anthropogenic landscapes provided they are not persecuted through hunting or retaliatory killings (Pruetz *et al.* 2002; Duvall 2008; Hockings *et al.* 2009, 2010). In agreement with McLennan (2008), this enforces the conservation potential of such habitats. Furthermore, chimpanzees are able to move between forest fragments and the communities do not appear overly isolated in central Cantanhez. We have yet to understand at what point habitat isolation and degradation make chimpanzees unable to disperse, but the prospects for the long-term viability of chimpanzees in CNP will be greatly improved if dispersal opportunities are maintained between major forests. Immigration into isolated communities that inhabit forest-farm matrices appears problematic for some populations of chimpanzees. At Bossou in Guinea, for example, there has been no female immigration into the community since research began 30 years ago (Sugiyama 2004). Special efforts should be made to preserve key forested areas and ensure that connecting areas do not become impassable through the presence of densely populated villages, large cashew plantations or wide, busy roads.

In CNP, an approach to conservation that relies exclusively on the exclusion of local people is out of the question. The benefits to local communities living alongside potentially problematic wildlife such as chimpanzees must, therefore, surpass the costs, even within the borders of officially protected national parks (Hill *et al.* 2002). In face of burgeoning human populations, areas protected for wildlife and ecosystem functioning need to consider human welfare, and the result is a shift in favor of protected areas that allow for local resource use, with many initiatives aiming to link protected areas to local socioeconomic development (Naughton-Treves *et al.* 2005). Although habituation for tourism (and research, see Wrangham and Ross 2008) might be one answer, it is often considered inappropriate where apes and people live in very close proximity (MacFie and Williamson 2010; McLennan and Hill 2010). In reality, chimpanzee conservation in anthropogenic habitats requires "novel strategies such as alternative income-generating projects and enrichment planting, developed with the full involvement of local communities and delivered with a strong educational emphasis" (McLennan 2008, pp.52).

Managing protected areas in developing countries presents profound challenges, given widespread conditions of poverty, rapid population growth, and political instability. Primates, particularly chimpanzees, are among the most visible elements of the biodiversity of Guinea-Bissau and have a key role to play as 'flagship' species to attract attention to the need for conservation of some of the most important natural habitats of the country (Gippoliti *et al*. 2003; Sousa and Frazão-Moreira 2010). Long-term conservation success in such protected areas and elsewhere requires concerted efforts to balance the requirements of humans and other primates in their shared environments.

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Gene Flow and Genetic Diversity of Chimpanzees in Tanzanian Habitats

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Abstract: Tanzania is located at the southeastern end of the eastern chimpanzee (*Pan troglodytes schweinfurthii*) distribution. Except for two national parks, their habitats have been degraded due to human activities. To clarify the gene flow and genetic diversity of chimpanzees in Tanzania, we analyzed the mitochondrial sequences of chimpanzees in six sites (Lwazi, Wansisi, Mahale, Karobwa, Ugalla-Masito, and Gombe), some of which are now isolated. The southernmost habitat (Lwazi) was about 150 km away from the nearest habitat but, considering the geographic distance, the genetic distance of the chimpanzees between Lwazi and the other habitats was not high. In contrast, the genetic distance between the chimpanzees in the northernmost habitat (Gombe), and the other habitats was relatively high considering the geographic distance. The results suggest that the Malagarasi River, which runs between Gombe and the southern habitats, limits gene flow. The genetic difference analyses also suggest that the habitats of Wansisi, Mahale, Karobwa, and Ugalla-Masito can be regarded as one population ("Greater Mahale"). The genetic distance between Lwazi and Gombe was lower than that between Gombe and the Greater Mahale habitats. This result suggests that early chimpanzees came to the Greater Mahale habitats through the southern habitats around Lwazi. The nucleotide diversity was not different from that in other countries, probably due to the sequence variety. There were unique haplotypes in several habitats where the number of chimpanzees was estimated to be small, which implies that some haplotypes are probably be at risk of disappearing. These data will be useful for conservation planning.

Keywords: Chimpanzee, gene flow, genetic diversity, Tanzania

Introduction

Environmental degradation, in this case, the loss, degradation and fragmentation of chimpanzee habitats through human activities, immigration and population growth, reduces and fragments their regional populations. Appropriate chimpanzee habitats become smaller and fragmented, making it difficult to determine the population distribution and gene flow before the advent of human activities. An understanding of the gene flow of animals between fragmented habitats is of great value for the design of conservation strategies.

The eastern chimpanzee (*Pan troglodytes schweinfurthii*), occurs in the Democratic Republic of the Congo (DRC), Uganda, Rwanda, Burundi, and the United Republic of Tanzania (Tanzania) (Inskipp 2005). The most recent estimate of the number of eastern chimpanzees was 76,000–120,000; most of them, 70,000–110,000, in DRC (Inskipp 2005). Tanzania, at the southern and eastern extremes of the distribution of *P. t. schweinfurthii*, is estimated to have a population of just 1,500–2,500 (Inskipp 2005). All wild Tanzanian chimpanzees live along the eastern shore of Lake Tanganyika and unfortunately face the threat of extinction (Bakusa and McManus 2005). Forest loss outside Gombe National Park has been estimated at 4% per year, and the annual growth rate of the human population in the Kigoma region (Fig. 1) has increased. Furthermore, many refugees from DRC, Burundi, and Rwanda have settled in western Tanzania (Whitaker 2002), having a negative impact on the chimpanzee populations in the area (Ogawa *et al*. 2006a).

Kano (1972) first reported the distribution of chimpanzees along the eastern shore of Lake Tanganyika in detail. Thereafter, other studies have been conducted (Massawe 1992; Zamma *et al*. 2004; Ogawa *et al*. 2006b), and Ogawa *et al.* (1997) identified another chimpanzee habitat, namely Lwazi, which marks the southernmost tip of their geographic range. Although no researchers have ever observed chimpanzees in this area, Ogawa *et al*. (1997) found 16 chimpanzee nests and two chimpanzee fecal samples; furthermore, the local people in the area have observed chimpanzees. We need to confirm whether the chimpanzees in Lwazi are in fact eastern chimpanzees and clarify their genetic backgrounds.

Yoshikawa *et al*. (2008) summarized the current distribution of chimpanzees and estimated the presence of four local populations: Gombe, Lilanshimba, Ugalla-Masito-Mukuyu-Mahale-Karobwa-Wansisi, and Lwazi. The number of chimpanzees outside the national parks of Gombe and Mahale has been estimated to be less than 700 (Yoshikawa *et al*. 2008). Today these four populations are isolated from each other, but we do not know the exact time when this happened.

Genetic studies can clarify the level of gene flow among populations. In the case of the great apes, rivers influence their distribution and their genetic structure (Eriksson *et al*. 2004; Anthony *et al*. 2007). The Ugalla River in western Tanzania is the eastern border of the chimpanzee geographic range (Fig. 1). In addition, the Malagarasi River, a large river in western Tanzania, may have limited gene flow (Fig. 1). The Malagarasi River is the second longest river in Tanzania and the largest river flowing into to Lake Tanganyika. The Rugufu River may also be a barrier to gene flow (Fig. 1). It is important to determine the genetic structure of the populations in these habitats to clarify the genetic diversity, including populations with a small number of chimpanzees (Yoshikawa *et al*. 2008).

A number of studies have examined gene flow among eastern chimpanzee habitats. Genetic divergence analysis has indicated that eastern chimpanzees expanded their range from eastern DRC in recent times; between 20,000 and 61,000 years ago (Goldberg and Ruvolo 1997a; Gagneux *et al*. 1999). Among the chimpanzees, it is the females rather than the males that typically disperse from their natal community (unit group) upon reaching maturity (Nishida 1979; Pusey 1979; Boesch and Boesch-Achermann 2000); this process influences the genetic structure within a community (Inoue *et al*. 2008). As expected from these findings, mitochondrial haplotypes were found to be shared by chimpanzees from different habitats, and they were not sorted into location-specific clusters (Morin *et al*. 1994; Goldberg and Ruvolo 1997b). Although there are some studies on the phylogenetics of the eastern chimpanzees that include samples from Tanzania (Morin *et al*. 1994; Goldberg and Ruvolo 1997b), they were taken from only a few sites.

In this study, we collected DNA samples non-invasively (feces, urine, and saliva) from eastern chimpanzees in six Tanzanian habitats. In all habitats except for the two national parks, it is difficult to observe chimpanzees and collect fresh samples, which would provide a relatively large amount of DNA compared with old samples. We analyzed mitochondrial DNA because PCR amplification of mitochondrial regions is easier than it is for nuclear DNA when dealing with degraded noninvasive samples. Using the sequence data, we examined the genetic structure and genetic diversity of chimpanzees in Tanzania in detail.

Materials and Methods

Samples

We collected noninvasive genetic samples from chimpanzees from six habitats in western Tanzania (Fig. 1). Eiji Inoue collected non-invasive samples, such as feces, urine, and saliva, of almost all chimpanzees of the M group at Mahale, which has been studied for more than 40 years (Nishida 1990; Inoue 2005; Inoue *et al*. 2008). Hideshi Ogawa collected fecal samples from around chimpanzee nests at Lwazi, Wansisi, Karobwa, Ugalla-Masito, and Gombe. The Malagarasi River runs between Gombe and the other habitats. Gombe and Lwazi are isolated from the other habitats (Yoshikawa *et al*. 2008). Yoshikawa *et al*. (2008) suggested that the chimpanzee habitats in Ugalla-Masito, Karobwa, Mahale, and Wansisi comprised one continuous population. We, therefore, defined this estimated population as the "Greater Mahale" population in this study.

DNA extraction and sequencing

DNA was extracted using either a QIAamp DNA Stool Mini Kit (Qiagen, California, USA), QIAamp DNA Mini Kit (Qiagen), QIAamp DNA Micro Kit (Qiagen), or ISOHAIR (Nippon Gene, Tokyo, Japan), depending on the sample, according to the manufacturers' instructions.

A 331-base-pair segment of the mitochondrial hypervariable control region was analyzed. We conducted polymerase chain reaction (PCR) amplification using the primers L16041 and H16498 (Morin *et al*. 1994; Eriksson *et al*. 2004) or the primers L16031 (5′-TAAACTATTCTCTGTTCTTTCA-3′) and H16405 (5′- CGGGATATTGATTTCACGGAGG-3′). The PCR products were purified and then directly sequenced using the dye termination method and an ABI 3100 sequencer (Applied Biosystems, California, USA).

Analyses

We used the mitochondrial sequence data of the eastern chimpanzees (*P. t. schweinfurthii*) from Uganda (Langergraber *et al*. 2007, EU077270-EU077418), Rwanda, and DRC (Keele *et al*. 2006, DQ370332-DQ370353) to construct a phylogenetic tree. Using MEGA 4.0 (Tamura *et al*. 2007), we aligned all the determined haplotypes including the data from other countries, trimmed the reference sequences to fit the determined sequences, and then removed the duplicate sequences from the same origin. We constructed a neighbor-joining tree including one sequence of central chimpanzees from Cameroon (*P. t. troglodytes*, DQ367534) as an outgroup (Saitou and Nei 1987; Tamura *et al*. 2004). The bootstrap values were calculated using MEGA 4.0 software. Genetic differentiation (F_{ST}), gene diversity, and nucleotide diversity were calculated with Arlequin ver. 3.0 (Nei and Li 1979; Excoffier *et al*. 2005). Statistical analyses of F_{ST} values were also conducted with Arlequin.

Results

Twenty-two haplotypes were detected among the 138 sequences obtained from the six habitats (Table 1). These sequences have been deposited in DDBJ/EMBL/GenBank under accession numbers AB677454–AB677475. Three of the five haplotypes from Lwazi were also found in other habitats. Haplotype B was found in all habitats excluding Gombe. All four haplotypes found in Gombe were unique. Ugalla-Masito, Karobwa, and Lwazi chimpanzees had nine, two, and two unique haplotypes, respectively.

Phylogenetic tree analyses revealed that mitochondrial haplotypes were shared by chimpanzees from different countries (Fig. 2). Almost all clusters included some

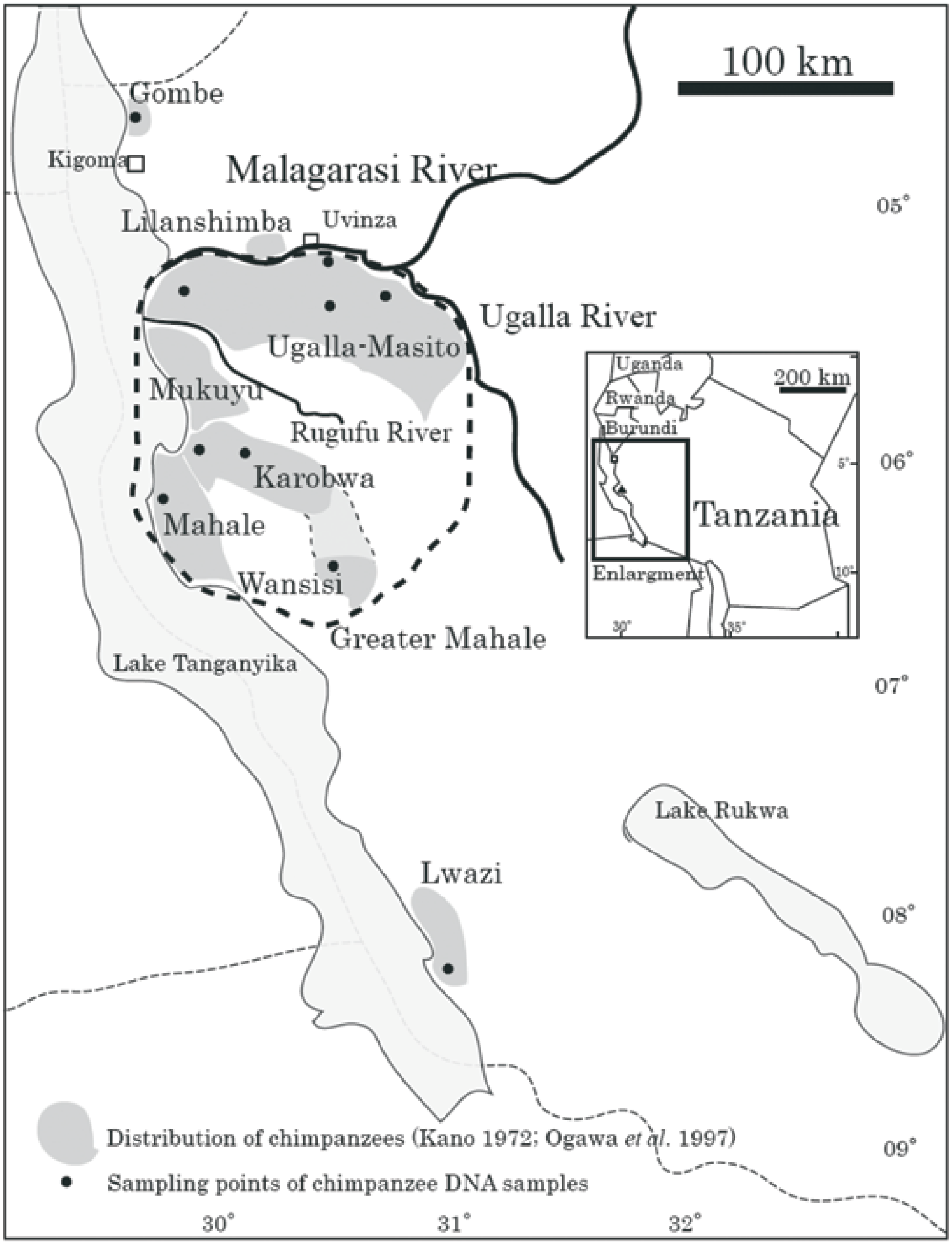

Figure 1. Distribution of chimpanzees and sampling sites in Tanzania. This figure was modified from Figure 1 in Yoshikawa *et al*. (2008). Using the data presented in their discussion, we connected the Karobwa and Wansisi habitats.

sequences from Tanzania, but the distribution of haplotypes was skewed. In total, eight of 22 haplotypes from Tanzania belonged to cluster IV, which had only one haplotype from Uganda. Among those eight, three major haplotypes (A, B, and D) were found in many samples in four or five Tanzanian habitats. The haplotypes from Gombe (S, T, U, and V) were similar to the other haplotypes from the other countries, but not to the other haplotypes from Tanzania.

The F_{ST} values among the habitats in the Greater Mahale population were low, and they were not significantly positive between Karobwa and the other habitats (Table 2). The F_{ST} values between Lwazi and the other habitats were lower

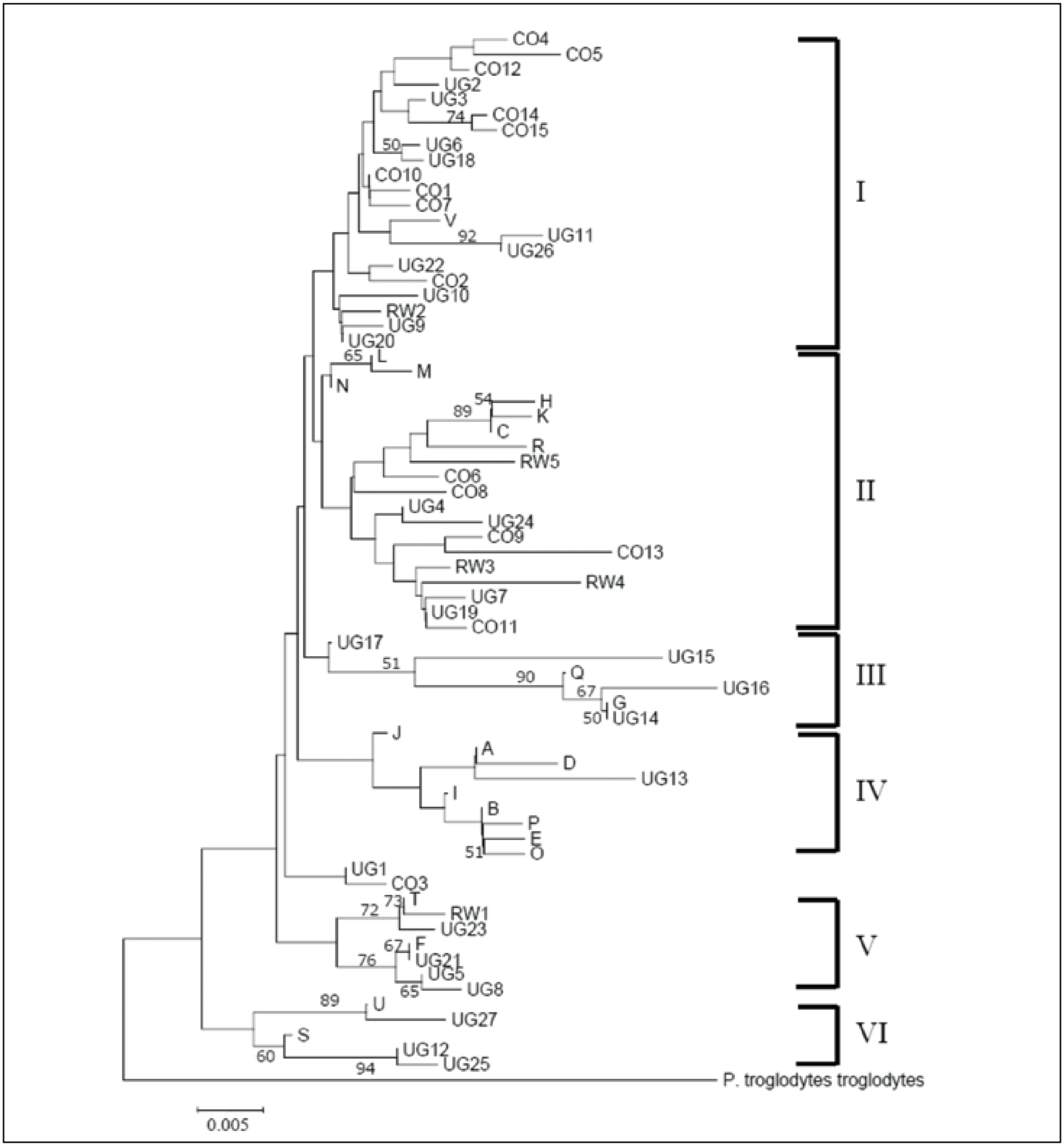

Figure 2. Phylogenetic tree using the neighbor-joining method. Bootstrap values ≥50% are shown above the relevant branches. A-V indicates the haplotypes found in this study (Table 1). The sequences beginning with CO, RW, and UG were those from DRC, Rwanda, and Uganda, respectively.

than those between Gombe and the other habitats. Figure 3 revealed no correlation between the geographic distance and F_{ST} (Pearson correlation coefficient, $r = 0.15$, $P = 0.60$). The F_{ST} values between Gombe and the other regions were relatively high considering the geographic distance (Fig. 3).

Table 3 shows the diversity in each habitat. Although the number of haplotypes was large in Ugalla-Masito, the gene and nucleotide diversity were similar among the habitats. Gene diversity was highest in Gombe and Karobwa (0.87) and lowest in Mahale (0.68), while nucleotide diversity was highest in Gombe (0.022) and lowest in Mahale (0.013).

Discussion

Lwazi population

We confirmed that the chimpanzee samples from Lwazi belonged to eastern chimpanzees (*P. t. schweinfurthii*) because the haplotypes of samples from Lwazi were shared by other eastern chimpanzees (Fig. 2). Three of five haplotypes found in Lwazi were shared by chimpanzees in other habitats (Table 1), and all haplotypes found in Lwazi were sorted into the same cluster as that of the other sequences of eastern chimpanzees. The F_{ST} values between Lwazi and other habitats in Greater Mahale were not high considering the large geographic distances between them (Fig. 3). These results suggest that chimpanzee habitats in Lwazi and Greater Mahale had been continuous until they were isolated from each other recently.

Gene flow of chimpanzees in Tanzania

The F_{ST} value and the geographic distance were not correlated (Fig. 3). This was probably due to the large difference in F_{ST} values of Gombe and the other habitats. Langergraber *et al*. (2011) found that the F_{ST} value between Mahale and Gombe was lower than those between Gombe and the habitats in Uganda, although the distance between Gombe and Uganda habitats was greater than 400 km. The result of the phylogenetic tree also confirmed this fact (Fig. 2). The unique haplotypes in Gombe (S, U, and V) are close to the sequences from Uganda but not to those from other Tanzanian habitats. Cluster IV contained many sequences from all habitats of Tanzania excluding Gombe but did not include those from the other countries. The probable barrier between Gombe and other Tanzanian habitats is the Malagarasi River, as has been reported in studies on the effect of rivers on the gene flow in other great apes (Eriksson *et al*. 2004; Anthony *et al*. 2007).

The genetic distance between Gombe and Lwazi was smaller than those between Gombe and the other habitats (Table 2), even though the geographic distance between Gombe and Lwazi was greater than those between Gombe and the others (Fig. 3). This may suggest that chimpanzees in Greater Mahale came through the southern habitats around Lwazi. Assuming that the geographic distances between Gombe and the habitats in Greater Mahale were the distances between Lwazi and Gombe plus the distances between Lwazi and the habitats in Greater Mahale, a positive significant correlation between genetic and geographic distances was found (Fig. 4, Pearson correlation coefficient, $r=0.85$, $P<0.001$). The actual pathway between Gombe and Lwazi was longer than the geographic distance between them

Table 1. Haplotype constitutions in Tanzanian habitats.

	Mitochondrial haplotype																						
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	Total
Lwazi	1	6	2		1	4																	14
Wansisi	1	3		2			4																10
Mahale	16	22	11	2																			51
Karobwa	3	1		3			1	1	1														10
Ugalla-Masito		22		5			3			1	1	3	1	2	1	1	1	1					42
Gombe																			1	2	1	2	6
	21	59	13	12	1	4	8	1	1	1	1	3	1	2	1	1	1	1	1	2	1	2	138

Table 2. FST values among Tanzanian habitats.

		Lwazi	**Greater Mahale**				**Gombe**
			Wansisi	Mahale	Karobwa	Ugalla-Masito	
Lwazi		-					
Greater Mahale	Wansisi	0.16	-				
	Mahale	0.07*	0.20	-			
	Karobwa	0.10*	0.03*	0.03*	-		
	Ugalla-Masito	0.07	0.10	0.05	0.04*	-	
Gombe		0.14	0.26	0.25	0.21	0.25	-

* No significant difference was found between two habitats (Exact test, $P > 0.05$)

because chimpanzees needed to avoid the Malagarasi River. Although it is difficult to determine the actual pathway, Figure 4 strongly suggests the path from Gombe to Greater Mahale was via Lwazi. This result indicates the importance of Lwazi habitats for understanding the expansion of chimpanzees in Tanzania. Genetic analyses of chimpanzees on the western shore of the Lake Tanganyika in DRC will provide important data on the history of eastern chimpanzees in the southern habitats.

The genetic structure within Greater Mahale was also clarified. Figure 4 shows that the genetic distance between Mahale and Wansisi was high for the geographic distance between them. Inferring from this result and the current distribution (Fig. 1), the direct gene flow between Mahale and Wansisi was limited, and Karobwa habitats connected them. A river that runs between Ugalla-Masito and Karobwa-Mahale-Wansisi, the Rugufu River, is another possible barrier to gene flow. The F_{ST} values between Ugalla-Masito and Karobwa-Mahale-Wansisi was low, and that between Ugalla-Masito and Karobwa was

Table 3. Genetic diversity among Tanzanian habitats.

Habitat		*N*	No. of haplotypes	Gene diversity	Nucleotide diversity
Lwazi		14	5	0.76	0.017
Greater Mahale	Wansisi	10	4	0.78	0.019
	Mahale	51	4	0.68	0.013
	Karobwa	10	6	0.87	0.017
	Ugalla-Masito	42	12	0.71	0.014
Gombe		6	4	0.87	0.022

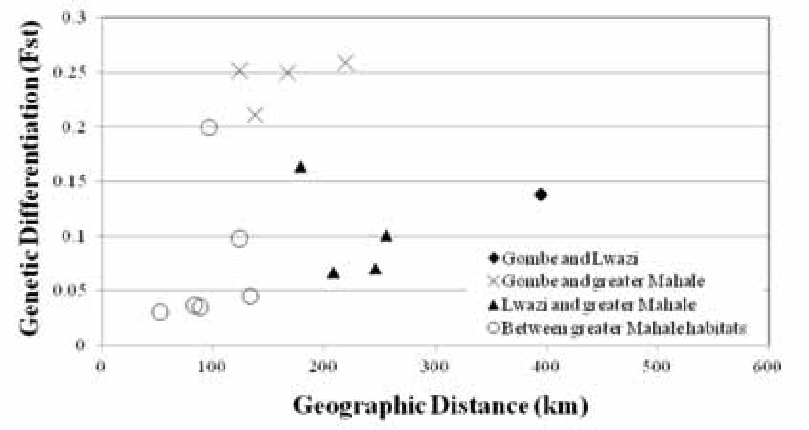

Figure 3. Relationship between the genetic and geographic distances.

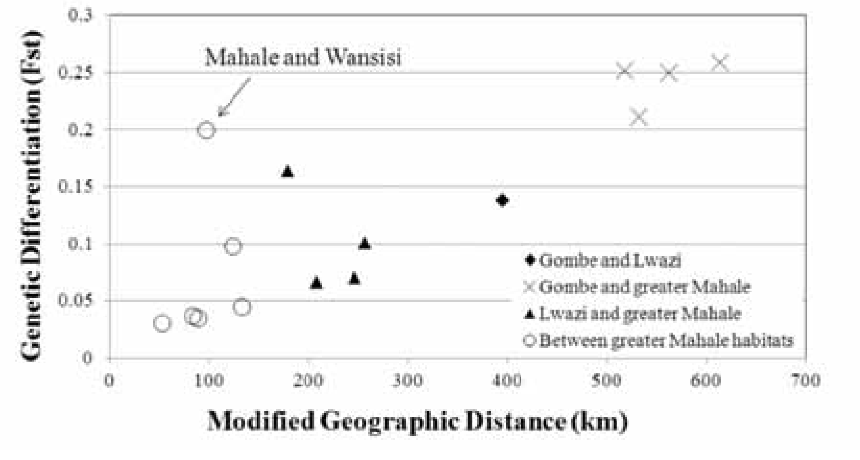

Figure 4. Relationship between the genetic and geographic distances with some modifications (see 'Discussion').

not significantly positive. These results suggested that gene flow has not been limited. The F_{ST} values among the habitats in Greater Mahale were low, and gene flow was not limited between Karobwa, which is located in the center of the Greater Mahale habitats, and the other habitats. These results confirmed that the Greater Mahale habitats can be regarded as one continuous population, estimated from the result of the current distribution (Yoshikawa *et al.* 2008).

Genetic diversity

Gombe exhibited the highest diversity among the habitats in Tanzania (Table 3). This result may reflect the low genetic diversity among the southern Tanzanian habitats, which mark the southeastern end of the chimpanzee's distribution, due to the limited gene flow between Gombe and these habitats. To evaluate this hypothesis, we compared the diversity in the southern Tanzanian habitats (Lwazi, Wansisi, Mahale, Karobwa, and Ugalla-Masito) to that in the 19 habitats of Uganda, DRC, and Rwanda reported by Goldberg (1998).

Although the range of gene diversity in the southern Tanzanian habitats (0.68–0.87) was similar to that in the other countries (0.64–1.02), gene diversity as such was significantly lower (Mann-Whitney U test, $P=0.04$). This significant difference was probably due to the small number of haplotypes in the southern Tanzanian habitats. We analyzed 51 individuals of the M group in Mahale but found only four haplotypes (Table 1). Langergraber *et al.* (2007) analyzed mitochondrial DNA of three chimpanzee communities in Uganda and found 14, 16, and seven haplotypes among 28, 94, and 20 individuals, respectively. Thus, there were fewer haplotypes per social community in southern Tanzania than in Uganda. In contrast, the nucleotide diversity was not different between the habitats in southern Tanzania and the other countries (Mann-Whitney U test, $P=0.21$). This probably reflected the fact that the sequences in southern Tanzania belonged to several clusters in the phylogenetic tree (Fig. 2). This also suggested that the southern Tanzanian chimpanzees have not experienced a severe bottleneck with respect to genetic diversity, resulting in the retention of sequence variety. Sequence variety is important for total genetic diversity in the southern Tanzanian habitats.

Unique haplotypes were found in Lwazi, Karobwa, Ugalla-Masito, and Gombe. The number of chimpanzees in those habitats is small (Pusey *et al.* 2007; Yoshikawa *et al.* 2008). Consequently, there are probably just a few individuals with unique haplotypes. Chimpanzees in an isolated and limited habitat are at risk of losing mitochondrial diversity, resulting in difficulty in suitable mating (Shimada *et al.* 2009). It is, therefore, important to maintain the habitats and population sizes of chimpanzees to preserve their diversity.

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The Indochinese Silvered Leaf Monkey *Trachypithecus germaini* (*sensu lato*) in Lao PDR

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Abstract: The Indochinese silvered leaf monkey *Trachypithecus germaini* (perhaps comprising two species, *T. germaini* [*sensu stricto*] and *T. margarita*) is probably the rarest and most threatened monkey in Lao PDR. It has received less conservation-related attention in the country, however, than have the primates endemic to Indochina east of the Mekong because until recently it was generally considered conspecific with the widespread *T. cristatus* of Sundaic South-east Asia. All Lao records with firm locality details are from south of 16°23'N (in Dong Phou Vieng National Protected Area) and in lowland forests (up to 550 m above sea level), with many from near waterbodies. The predominant habitat seems to be semi-evergreen forest as patches and strips within a mosaic of more deciduous forest types, especially semi-evergreen forest in riparian and other waterside situations. Occupied semi-evergreen forest seems generally at the dry end of its spectrum, with a high deciduous tree component (this is the predominant type in interior plains-level Indochina), where this forest type grades to what some call mixed deciduous forest. Few if any records come from the interior of extensive unbroken semi-evergreen forest, or from highly-deciduous mixed-deciduous forest. Occupied areas include narrow stands flanking watercourses in deciduous dipterocarp forest, but there are no records from the more extensive deciduous dipterocarp forest matrix itself. Vague reports suggest occurrence up to 1,200 m, but given the high survey effort in such habitat, the species is at best very rare above the lowlands. Lao villager reports, and comparison with its status in similar habitats in adjacent Cambodia, suggest steep declines in Lao PDR. Suitable habitat (as profiled above) naturally covers only a small part of the southern Lao landscape, is among Lao PDR's most threatened habitats, and bears heavy hunting. Hence the great rarity of Indochinese silvered leaf monkeys compared with sympatric monkeys and gibbons, which inhabit the more extensive hill forests. There are records of the Indochinese silvered leaf monkey from only one Lao site since 2001. Although appropriate surveys during the 2000s have been limited, the species may now be extremely rare in the country and should join other, better publicized, bird and mammal species of these southern lowland plains landscapes as in need of urgent conservation action.

Key Words: Conservation status, distribution, habitat, Laos, *Trachypithecus margarita*, *Trachypithecus villosus*

Introduction

Lao People's Democratic Republic (Lao PDR; Laos), a land-locked country of 236,800 km² in South-east Asia, supports a rich primate fauna comprising *c.*15 species, depending on taxonomy. Several of these primates are of obvious international conservation concern because of their restricted geographic ranges, living only east of the Mekong, and in some cases only in small parts of that area: pygmy loris *Nycticebus pygmaeus*; red-shanked douc *Pygathrix nemaeus*; François'-group leaf monkey *Trachypithecus francoisi* (*sensu lato*), of which there are several distinct forms; and various gibbons *Nomascus*. These species have, understandably, dominated the common thinking about Lao primate conservation, and detailed national status overviews have been prepared for these monkeys (Timmins and Duckworth 1999; Duckworth *et al*. 2010; Steinmetz *et al*. 2011) and for Lao gibbons (Duckworth 2008; Boonratana *et al*. in press). A further Lao primate which has to date received little attention is a gray leaf monkey *Trachypithecus* occurring in the southern third of the country. During the 1950s–1990s, its populations in Lao PDR (and neighboring Thailand, Cambodia and Vietnam) were almost universally considered conspecific with the relatively well-known, widespread and numerous silvered leaf monkey *T. cristatus* of Sundaic South-east Asia (the Malay peninsula, Borneo, Sumatra and associated small islands).

Morphological and genetic characters both suggest, however, that these Sundaic and non-Sundaic populations are not conspecific, although this view is not universal: Brandon-Jones *et al*. (2004) continued to treat them as one species, which they called *T. villosus*. Groves (2001, 2005) used the name *T. germaini* for the non-Sundaic populations, inhabiting southern Vietnam, Cambodia, much of Thailand and perhaps adjacent Myanmar, as well as Lao PDR. Nadler *et al*. (2005), followed by Roos *et al*. (2008) and Francis (2008), divided these non-Sundaic populations into two species, suggesting that *T. germaini* (*sensu stricto*) lived west of the Mekong and *T. margarita* to the east. Morphological differences between the taxa were proposed (illustrated by Nadler *et al*. 2005), but sample sizes and intra-taxon variation were not discussed, hindering independent evaluation of the taxonomic conclusions. Brandon-Jones *et al*. (2004) had recognized these two taxa as subspecies, and assigned two specimens from Thailand west of the Mekong to *margarita*. Nadler *et al*. (2005) implicitly disagreed with the identification of one of these records and accounted for the other (and some more from west of the Mekong purportedly of *margarita*, from southern Vietnam) through confusion over original provenance, a problem not uncommon with primate records (Brockelman and Ali 1987).

Nadler *et al*. (2005, 2007, 2008) and Groves (2007) underlined the urgent need for more data relevant to this proposed division of the non-Sundaic silvered leaf monkeys into two species, and in particular the speculation that the Mekong forms the barrier between them. Observations of external morphology during 2006–2007 surveys along the Mekong in northern Cambodia (for example, Timmins 2008) show that the Mekong does not make a clear division. Resemblance to the two purported forms (based on relative contrast of extremities and circum-orbital coloration) varied, often considerably, within groups, even allowing for perception effects of viewing conditions. Moreover, observations in 1998 and 2000 in northeastern Cambodia (Timmins and Men 1998; Timmins and Ou 2001) involved sightings of *germaini* (*sensu stricto*)-like animals (retrospective identification) east of the Mekong, up to 20 km "inland" (at 13°11'N, 106°15'E). Seeing the Mekong as a barrier is too simplistic if these pelage characters have taxonomic relevance. Several lengthy reaches of the Mekong in southern Lao PDR and especially Cambodia have extensive braiding, including many secondary seasonal channels and islands, and the main channel has switched course over time (Meijaard and Groves 2006), allowing populations to change from one side of the river to another.

Francis (2008) noted the likelihood that both Indochinese taxa were severely threatened by habitat loss and hunting, urging clarification of current status: *T. germaini* (*sensu lato*) is considered Endangered on *The IUCN Red List of Threatened Species* (Nadler *et al*. 2008). Here we review information from Lao PDR concerning the Indochinese silvered leaf monkey to determine its range and conservation status in the country. Most of the records reviewed here have not previously been published in detail, although text overviews and verbal summations incorporating most of them have informed review sources such as Duckworth *et al*. (1999) and Nadler *et al*. (2003, 2005, 2008).

Conventions

All Lao populations are treated, as in *The IUCN Red List of Threatened Species* (Nadler *et al*. 2008), as *T. germaini*: the analyses recognizing *T. margarita* (Nadler *et al*. 2005; Roos *et al*. 2008) used no samples from Lao PDR; no modern pelage specimens are available from the country; and the paucity of historical specimens (Table 1) prevents confident identification as *germaini* (*sensu stricto*) or *margarita* inferred through location.

Areas and sites referred to in the text are marked on Figure 1. Place names are based on the 1985–1987 series of 1:100,000 maps of the RDP Lao Service Géographique d'État (RDPL SGE) maps with the minor modifications of Thewlis *et al*. (1998). Where there is no RDPL SGE map-name, the name in local usage is given, transliterated according to the original observer. Coordinates and altitudes, except where stated, are derived from the RDPL SGE maps. Considerable location detail accompanies the records (Appendix), following the urging of Brockelman and Ali (1987) for such precision in primate records.

Lao words incorporated in place-names: *Ban* = village (here, meaning the area surrounding the village, rather than the village itself); *Houay* = stream; *Keng* = rapids; *Nam* = river; *Nong* = pool; *Pak* = river-mouth; *Phou* = mountain or hill; *Xe* = river.

Table 1. Historical (pre-1990) specimens of the Indochinese silvered leaf monkey from Lao PDR.

Location	Coordinates (approx.)	Date	Specimen	Reference
Bolaven plateau[1]	15°26'N, 106°23'E	6 February 1932	AMNH 87259	Fooden 1976; D. P. Lunde *in litt*. 2007
Ban Phon	15°25'N, 106°42'E	28 November 1931	FMNH 38014	[2]Brandon-Jones *et al*. 2004
Ban Phon	15°25'N, 106°42'E	22 January 1932	FMNH 38015	[2]Brandon-Jones *et al*. 2004

[1]Fooden (1976) gave 15°10'N, 106°20'E, a roughly central point for the Bolaven plateau, for this specimen, but Legendre specimens from the "Bolaven plateau" nearly all came from Ban Thateng (Legendre 1932, 1936); most were purchased from local people and their precise origin is unknown (see text).

[2]Also listed, as *argenteus*, by Osgood (1932); assigned to *margarita* by Brandon-Jones *et al*. (2004).

Methods

Direct-observation general large mammal survey-effort across Lao PDR during 1992–2007 was summarized by Timmins and Duckworth (1999, 2008) citing the original, often internal, reports from each. Mammal-related information-gathering activities with little opportunity to generate reliably identified locality records of this monkey (for example, village-based activities, training activities, camera-trapping and trade studies) are not covered by these summations. Most of the relevant surveys consisted of a few weeks to a few months of direct observation to assess general habitat type and condition, and to seek by direct observation (mostly during daylight, and including hunted remains) birds and large mammals (generally, those identifiable without specimens) of high national and, especially, global conservation concern. Monkeys were thus among the best covered groups of mammals. These surveys were supplemented by appeals to colleagues for records, and the authors' own surveys after 2008.

Identification in Lao PDR of gray leaf monkeys as *T. germaini* needs care, because another gray species, Phayre's leaf monkey *T. phayrei* (also of disputed taxonomy), inhabits the country. There are too few Lao specimens of gray leaf monkeys to define even the coarse ranges of both these species (Table 1, Fig. 1; also Timmins *et al*. in press). Although the two are readily separated when seen well, monkeys recorded during 1990s–2000s surveys in Lao PDR were typically shy, so views were often brief and partly obscured. Therefore, identification of all field records from these decades has been checked during preparation of this review, in particular to isolate where the original identification as silvered was simply inferred through locality. Additionally, two records (one provisional) of animals in villages were in error. Evans *et al*. (2000, p.78) wrote of a captive youngster, "believed to be this species" on the Bolaven plateau, in Ban Nongmek (15°10'N, 106°32'E), which "reportedly came from nearby". Several photographs of the young colobine in the village, taken on 19 February 1995, were found in the archives of the Wildlife Conservation Society Lao office in mid 2010: they

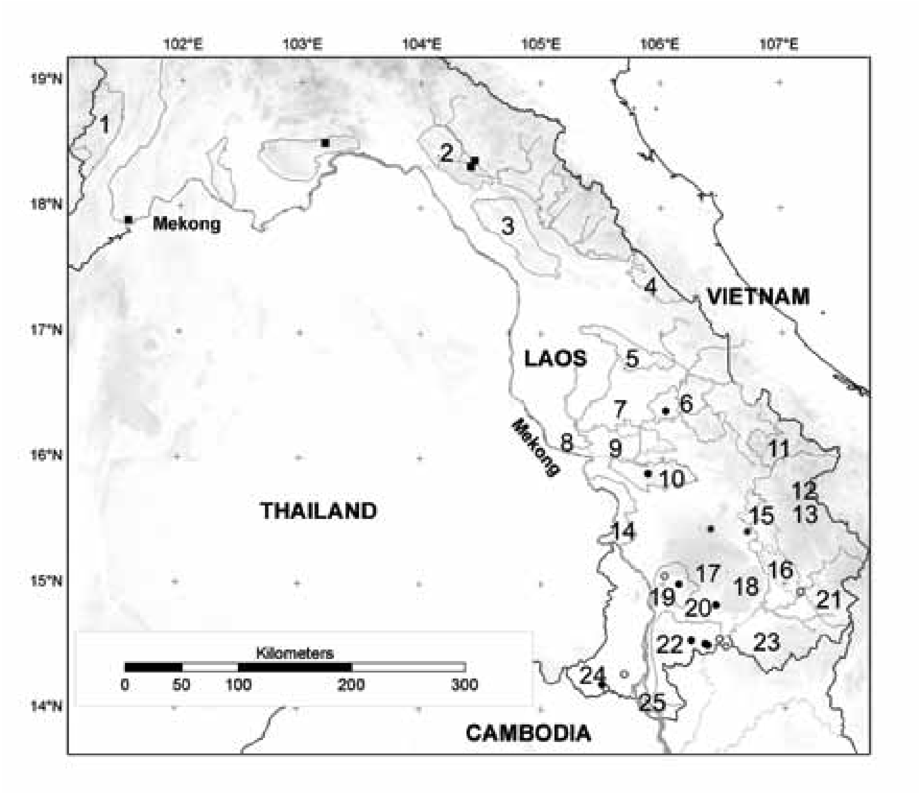

Figure 1. Lao PDR, showing localities mentioned in the text and records. Background shading shows altitude, darker areas being higher. All national protected areas (NPAs) within the area covered, but only those national production forest areas (PFAs) referred to in the text, are shown.

● modern record of the Indochinese silvered leaf monkey, identification confirmed;

○ modern record of the Indochinese silvered leaf monkey, identification provisional;

* historical record of the Indochinese silvered leaf monkey, identity confirmed, locality imprecise;

■ southernmost records of Phayre's Leaf Monkey in Lao PDR.

Numbered areas: 1, Nam Pouy NPA; 2, Nam Kading NPA; 3, Phou Hinpoun NPA; 4, Hin Namno NPA; 5, Phou Xang He NPA; 6, Dong Phou Vieng NPA; 7, Xonbouly Eld's Deer Sanctuary; 8, Xe Banghiang and major tributaries; 9, Dong Sithouan PFA; 10, Xe Bang-Nouan NPA; 11, Xe Sap NPA; 12, Phou Ahyon; 13, Dakchung plateau; 14, Phou Xiang Thong NPA; 15, Houay Pen PFA; 16, Nam Pa PFA; 17, Bolaven plateau; 18, Xe Namnoy headwaters; 19, Dong Hua Sao NPA; 20, Bolaven Southwest pNPA; 21, Dong Ampham NPA; 22, Xe Pian NPA; 23, Nam Ghong Provincial Protected Area; 24, Dong Khanthung NPA; 25, Siphandon.

clearly show a young red-shanked douc. Secondly, in December 1993, Bergmans (1995) purchased a colobine skull (no lower jaw, or upper incisors or canines) in Ban Tangyeung (Dakchung plateau, 15°30'N, 107°02'E) that was reportedly hunted nearby; all land lies above 1,040 m. The skull (ZMA 24.918) is from a douc, based on the "greater depth [than in *Trachypithecus*] of its choana or posterior nares (i.e., the rear opening of the nasal aperture below the cranium)" (D. Brandon-Jones *in litt*. 2010; see also Pocock 1935) evident in comparison with specimens of both genera held at the Natural History Museum, London, by P. D. Jenkins and JWD, corroborated by D. Brandon-Jones's examination of photographs. Its youth (its last molar is not yet erupting), gives it a superficial resemblance to *Trachypithecus* in some characters.

Reliable identification of *T. germaini* using local names is impossible in Lao PDR. Echoing similar problems elsewhere (Nadler *et al*. 2005), Duckworth *et al*. (2010) discussed the difficulties of this activity with colobines in Lao PDR. The name *taloung* in wide use in the southern half of Lao PDR is commonly associated with this species, but is probably best seen as meaning simply *Trachypithecus*: in the north of its area of use, around Phou Hinpoun National Protected Area (NPA) and perhaps Nam Kading NPA, it is apparently used for François'-group leaf monkey *T.* (*francoisi*) *ebenus* and perhaps *laotum* and Phayre's leaf monkey (Duckworth *et al*. 2010), and the sometime perception of a tight linkage of *taloung* with the Indochinese silvered leaf monkey probably simply reflects that the latter is the only species of *Trachypithecus* known in Lao PDR south of Savannakhet province. In Lao PDR north of Vientiane, *khang* is generally used for gray leaf monkeys, which in that part of the country are all Phayre's leaf monkeys, as far as is known (Timmins *et al*. in press). There are too few direct validations of local name usage for gray leaf monkeys to speculate on whether the transition from *taloung* in the south to *khang* in the north generally reflects that from Indochinese silvered to Phayre's leaf monkey. Because *khang* also seems to be used locally for François'-group leaf monkey (Duckworth *et al*. 2010), it is quite likely that relative usage of *taloung* and *khang* says more about human language patterns than about monkey species distributions. A further complication is that in Thailand *khang*, pronounced with a longer "a" sound, and perhaps more intuitively written as "khaang", is used as a general term for leaf monkeys. RB recorded apparent such usage in Lao PDR, around Dong Hua Sao NPA in 1997, during pre-survey discussions of mammals likely to live in the area; a few months later in this area, the animals in view were referred to as *taloung*. Such non-specific usage of *khang* is likely to become more frequent in Lao PDR, particularly among the urban sector receiving higher education, and reflecting greater use by Lao citizens of Thai wildlife books, Thai television and training institutes in Thailand.

Morphological notes

Descriptive notes relevant to identification come only from Xe Pian NPA, Bolaven Southwest pNPA and Dong Phou Vieng NPA (records as detailed in the Appendix). In Xe Pian NPA, a young animal seen in December 2000 (Fig. 2) had already molted into a gray coat and its pattern fitted '*margarita*', including the generally pale gray head, body and tail, with blackish patch on forehead, lower forelimbs and paws, and contrasting pale rings around the eyes. Of the animals seen in 1992, none of which allowed for a particularly good view, the faces were noted as "various shades of gray", and one was suspected to have a paler underside to the body; on another the hands were darker than the arms. This mix does not clearly fit either '*margarita*' or *T. germaini* (*sensu stricto*). The larger group on 5 March 1993 had limbs black from the elbow/knee to the soles of feet and hands, and almost entirely black tails, with the body pelage gray, mixing silver, ashy and sooty; some had darker backs, some had dense guard hairs of silver. The foreheads were black, the facial skin darkish. These broadly fit '*margarita*', although uniform black shanks are not consistent with information in Nadler *et al*. (2005) or later observations in Dong Phou Vieng NPA. The group seen in Bolaven Southwest pNPA on 17 April 1995 was of animals basically gray, darker on body than limbs, and thus consistent with nominate *T. germaini* (*sensu stricto*), not '*margarita*'. In none of these field observations was any note made of the eyes having pale spectacles. All these notes were taken unaware of features to distinguish between these two forms of Indochinese silvered leaf monkey; none allows conclusive identification.

The morphology of the animals in Dong Phou Vieng NPA was checked carefully in August 2010 against features in Nadler *et al*. (2005). The animals were seen well (for about ten minutes spread across half an hour, at 150–200 feet range) and resembled closely '*margarita*' as portrayed in Nadler *et al*. (2005; Figs 6 and 12). Specifically, the feet, hands and lower arms (but not the legs) were blackish, contrasting strongly with the gray body; this was much paler ventrally

Figure 2. Captive young Indochinese silvered leaf monkey *Trachypithecus germaini*, showing characters of '*margarita*', beside the Xe (= River) Pian, Xe Pian National Protected Area, December 2000. Photograph by G. Marris.

than dorsally, but the latter had abundant long silvery-white guard hairs giving it a muddy-gray overall tone. Blackish hair was also visible around the ears and sometimes on the forehead, although less prominently than in Nadler *et al*. (2005; Fig. 6): the long silvery hairs projecting horizontally from the forehead hid the black under-hair from some angles. These long hairs were also abundant sideways from the cheeks, down the nape, as an all-round beard and, with shorter and probably sparser hairs, as a moustache. There was, however, no hint of a vertical crest from the crown, in contrast to the luxuriant such growths depicted in Francis's (2008) drawings for both *margarita* and *germaini* (*sensu stricto*). The tail seemed darker on the upperside than under. The facial skin was blackish with distinct pale-fleshy colored spectacles, somewhat narrower than on Nadler *et al*. (2005: fig. 6); there was no pale skin around the mouth. Bare skin between the legs was also pale flesh in tone, as was the penis on the single male on which it was seen. Paw and limb characters were assessed on four adults, but the face critically on only one.

Habitat use

All Indochinese silvered leaf monkey records in Lao PDR with precise habitat information (given in the Appendix) were from forms of semi-evergreen forest or its degraded derivatives, in areas with uneven canopy (Fig. 3). Occupied areas were typically as patches and strips within a mosaic of more deciduous forest types, especially in riparian and other waterside situations. Where noted, occupied semi-evergreen forest was generally at the dry end of its spectrum, with a high deciduous tree component (as is the predominant form in plains-level locations in inland Indochina). Such forest grades into what some botanists consider a separate formation, mixed deciduous forest. In Cambodia many records come from habitat best described as mixed deciduous forest, but at the least deciduous end of its spectrum, and usually in association with wetland/riparian situations (RJT). Few if any records come from the interior of extensive unbroken semi-evergreen forest, or from highly deciduous mixed deciduous forest. Despite high survey effort, none was found in deciduous dipterocarp forest. This latter is extensive in the species's Lao range, and various records were from semi-evergreen gallery forests running through such habitat (for example, the Xe Kong plains sector of Xe Pian NPA). The paucity of records from the very large (*c*.1,500 km²), contiguous, "main block" of closed-canopy lowland semi-evergreen forest in Xe Pian NPA probably indicates, given the high survey effort (which in 1992–1993 was much more intensive than in the NPA's other habitats), a natural scarcity of such habitats unless in mosaic with more open forests. Indeed, the only main block record comes from the Houay Kua salt-licks, the largest area of broken-canopied and generally more open forest in the block. That these monkeys had previously been common but were almost hunted out from the main block by 1992 seems unlikely, given the large populations of similarly hunting-sensitive black giant squirrel *Ratufa bicolor* and gibbons in the main block on the 1992–1993 survey (Duckworth *et al*. 1994) and the number of leaf monkey sightings at that time in the more open and thus more easily hunted habitat of the NPA's Xe Kong plains.

Figure 3. Habitat typical of *T. germaini*: level lowland forest with open canopy. Ban Vangsikeo, Dong Phou Vieng National Protected Area; 6 November 2007. Photograph by D. Van Gansberghe.

Most Lao sightings came from within ½ km of waterbodies (11 of the 12 with adequate information, excluding repeat sightings of one troop; Appendix). This pattern is probably not an artifact, given the many records of other monkey species on these southern Lao surveys well away from rivers or pools (Timmins and Duckworth 1999, for douc; others not documented in detail yet). A number of records were, however, specifically noted as several kilometers from the nearest canopy-breaking stream (see site accounts). Speculations that this species is associated with rivers may well be true (particularly if narrow streams are included), but so far lack strong evidentiary basis in Lao PDR.

Most of the modern records come from lowland plains: the two highest confirmed sites are at only 550 m and 340 m (Appendix). The historical specimen location of Ban Phon (Table 1) is amid lowland habitat typical of modern records. Hunters' reports suggest this monkey can live up to 1,200 m or so in Xe Sap NPA (Appendix), but cannot be taken as proof of this. Even if gray leaf monkeys do occur in these hills, it cannot be discounted that they are Phayre's leaf monkeys unexpectedly far south. Indeed, J.-P. Pédrono (verbally 2010), long-term resident in Lao PDR, said that a leaf monkey was locally common on the Bolaven plateau, in the evergreen forest on the higher mountains, during 1956–1961 when he lived on a farm there. However, he recalled this monkey, which is not represented in his hunting photographs, as blue-gray in pelage and with prominent pale spectacles, characters better fitting Phayre's than the Indochinese silvered. Two 1990s claims of Indochinese silvered leaf monkeys from the Lao mountains were identification errors (see "Methods"), and while the identity of the historical "Bolaven" specimen as Indochinese silvered is not in doubt, it cannot be taken as evidence of highland occurrence. Even its rough altitude cannot be inferred, because the expedition in question in this area purchased many animals from visiting people (Legendre 1932, 1936). At this time there was easy road access to the lowlands from Ban Thateng, their collection base, and the collection includes various other predominantly lowland species.

Several local informants in Nam Pa PFA in 2010 specifically contrasted to JWD and Chaynoy Sisomphone (Division of Forest Resource Conservation, Department of Forestry, Vientiane) the status of *taloung* with that of *thani* (= gibbon) and *khadeng* (= douc), saying that the latter two lived deep in the hill (semi-)evergreen forest (which is extensive) and thus many animals remained, whereas the former did not occupy such areas and so, because the plains were so encroached, was rare. Moreover, all four areas with multiple sightings (Dong Phou Vieng NPA, Bolaven Southwest pNPA, Xe Pian NPA and Dong Khanthung pNPA; Appendix) are or contain lowland regions with extensive gentle terrain.

The high 1990s survey effort in the closed (semi-) evergreen hill forests that comprise much of the NPA area in southern Lao PDR, gave many sightings of other monkeys (Timmins and Duckworth 1999, for red-shanked douc; not published in detail for the other species): the lack of records in those forests of the Indochinese silvered leaf monkey shows it to be at best very rare in them. In sum, in Lao PDR the species seems not generally to occupy rugged hill ranges.

Distribution

The Indochinese silvered leaf monkey inhabits Lao PDR from its southernmost extent north to at least the Xe Banghiang catchment (including north of the main stream) at 16°23'N, in Dong Phou Vieng NPA (Fig. 1). It remains to be clarified whether it occurs even further north in Lao PDR. Boonratana (1998b) listed the species from Nam Pouy (= Nam Phoun) NPA, far to the north (based on a sighting near Ban Mai of at least 22 individuals [at least six adult females with four clinging infants] on 10 March 1998, in mixed deciduous forest at *c*.18°30'N, 101°22'E; *c*.300 m above sea level; RB) but adjusted the identification to provisional in Duckworth *et al*. (1999); no notes on appearance were taken. There has been no subsequent documentation of gray leaf monkeys from this part of Lao PDR, and their specific identity remains unknown.

The Indochinese silvered leaf monkey's apparent northern limit in Vietnam is rather similar, at 16°37'N; the provenance of animals collected there is not certain, and the northernmost solid record is from only 14°30'N (Nadler *et al*. 2003, 2005). The northernmost Thai record traced by Geissmann *et al*. (2004) was at *c*.15°30'N, with a fair number of leaf monkey records in the next degree north being all of Phayre's.

The southern boundary of Lao PDR's other gray colobine, Phayre's leaf monkey, is also unclear. The most southerly and southeasterly certain records traced by Timmins *et al*. (in press; included on Fig. 1 here) are from Khet Dong Hieng (17°53'N, 101°34'E; Fooden 1976) and Nam Kading NPA (18°20'N, 104°25'E), but interview records suggest occurrence south to Hin Namno NPA (17°34'N, 105°48'E). There is, therefore, a wide swathe (almost 2° of latitude; Fig. 1) across the central part of Lao PDR with no solid record of either gray leaf monkey species. If gray leaf monkeys do inhabit this area, they must be scarce, given the heavy direct survey effort in this part of the country, including remote areas with many direct sightings of other monkeys (for example, Timmins and Duckworth 1999). There is a similar latitudinal gap (at least 16°37'–17°53'N) between the recorded distribution of Indochinese silvered and Phayre's leaf monkeys in Vietnam (Fooden 1996; Nadler *et al*. 2003; Groves 2007), but apparently a very close approach in Thailand (Fooden 1976, Geissmann *et al*. 2004).

Fooden (1976) implied that this gap reflected general allopatry among *Trachypithecus*, and so because François'-group leaf monkey occurred in this latitudinal area, a gray leaf monkey might not be expected. However, this alone cannot explain the pattern, because away from karsts François'-group leaf monkey is highly localized, resulting in large tracts of central Lao forest today without any *Trachypithecus* records. In Lao PDR, this lacuna in gray leaf monkey distribution corresponds fairly closely to the distribution of red-shanked douc as portrayed in Timmins and Duckworth (1999). There is some co-occurrence of gray leaf monkeys with the douc at coarse geographic scale; at least Dong Phou Vieng, Xe Bang-Nouan and Dong Hua Sao NPAs hold both, but there are too few precise locality records to determine the extent of overlap in altitude and habitat, and no proof that it occurs at all. (In Cambodia there is, however, some overlap, with black-shanked douc *Pygathrix nigripes* occurring in Indochinese silvered leaf monkey's main habitat, but not, apparently, the leaf monkey extending into the douc's main habitat; for example, Timmins and Ou [2001].) Notably, in contrast to Vietnam and Lao PDR, red-shanked Douc does not occur in Thailand, where these two gray leaf monkey species' ranges abut.

The red-shanked douc has not been recorded down in the highly deciduous semi-evergreen forests of the Lao Mekong plain (Timmins and Duckworth 1999); it is plausible that these hold only gray leaf monkeys. However, plains forest north of the Bolaven plateau is now present only as small, degraded fragments from which most of the hunting-sensitive large vertebrates have been eradicated, and so it may never be possible to determine the natural distribution of primates there.

Abundance

Perhaps the most startling result concerning the Indochinese silvered leaf monkey in Lao PDR is the number of wildlife surveys within its range by experienced surveyors that did not record it, even though some lasted several weeks, and, usually, recorded other monkeys multiple times: Dong Phou Vieng NPA in 1997 (Appendix); the Dakchung plateau and Phou Ahyon in 1996 (Timmins and Vongkhamheng 1996a); Houay Pen PFA and adjacent protection forest in 2009 (Timmins 2009); Phou Xiang Thong NPA in 1996 (Evans *et al*. 1996a) and 1997 (Boonratana 1998a); Dong Hua Sao NPA in 1993 (Duckworth *et al*. 1994); Nam Pa PFA (then known as

Phou Kathong pNPA) in 1997 (Davidson *et al*. 1997); southern Attapu province in 1997 (Schaller 1997); Xe Kong plains of Xe Pian NPA in 2005 (M. R. Bezuijen 2006, *in litt*. 2010); and Dong Khanthung pNPA in 1996 (Timmins and Vongkhamheng 1996b). Moreover, P. Cunningham (*in litt*. 2010) never came across the species despite living throughout 1997 in the Siphandon (= "four-thousand islands") stretch of the Mekong adjoining Cambodia: yet Mekong bank and island forest support fair numbers of these monkeys in the wilder stretches of the river downstream in Cambodia (Timmins 2008).

Four of the 11 surveys which did find these monkeys (Appendix) had records only of hunted animals: Dong Hua Sao NPA 1996, Xe Pian NPA 1997 and 2000, and Dong Khanthung pNPA 1998. Even on the seven surveys with direct field sightings (Appendix), only three (Bolaven Southwest pNPA in 1995, Xe Pian NPA in 1992–1993 and Dong Khanthung pNPA in 1997) generated more than one record. Although Xe Pian NPA in 1992–1993 had the most records of any survey, that there were only four encounters indicates extreme rarity in the areas surveyed, when taking into account the enormous survey effort (62 person-weeks; Timmins and Duckworth 1999: Table I).

By contrast, red-shanked doucs were seen regularly during many surveys comparable in search effort (Timmins and Duckworth 1999). In sum, this general paucity of sightings of the Indochinese silvered leaf monkey suggests that it is typically scarce in its Lao range.

Conservation status

The Indochinese silvered leaf monkey is probably the rarest and most threatened monkey in Lao PDR. No survey has found a population at even moderate density over a large area. This forest-dependent species seems to be naturally localized and, at best, very scarce on rugged terrain: it is implausible that it could have been severely reduced by hunting in areas where black giant squirrel, red-shanked douc and gibbons remain relatively numerous. By contrast, the numbers documented lower down the Mekong in Cambodia (Timmins and Ou 2001; Timmins 2008) suggest that the species would not naturally be scarce throughout the Lao plains, but that in suitable habitats there it had been heavily reduced by hunting even by the early 1990s. The large populations of red-shanked doucs surviving in Lao PDR reflect not active conservation management, but the persistence of large rugged tracts of hill forest into which access, particularly for carrying out heavy items like ordinary-value wildlife meat, is laborious (Timmins and Duckworth 1999). There is little similar natural protection for Indochinese silvered leaf monkey habitat in Lao PDR: rivers are much used for transport and fishing, and their plains are more sought for agriculture than are steep slopes (for example, Thewlis *et al*. 1998). Riparian habitat is naturally linear, and because most of Lao PDR is rugged, in any given area there is generally less plains habitat to start with than there is hill forest. The extensive plains in the southern half of Lao PDR (Fig. 1) have been heavily converted for agriculture and areas not yet cleared are mostly deciduous dipterocarp forest, which does not support this monkey except along riparian semi-evergreen forests.

Hunting is intense throughout Lao PDR, including for arboreal diurnal primates (Duckworth 2008 and references therein). A recent wildlife trade study in Attapu province (Singh *et al*. 2006), based mostly on interview, concluded that this monkey is traded; the low numbers suspected by that study probably indicate rarity, not lack of buyer interest. Trade-driven hunting of general wildlife meat is likely to be a threat throughout its Lao range. This monkey is legally totally protected from hunting and trade throughout Lao PDR, but enforcement of the laws, particularly within the NPA system, is an urgent priority for it. There is no evidence of directed hunting for this species, but appropriate survey effort has been too low to be sure that it does not occur.

At Ban Vangsikeo (Dong Phou Vieng NPA), reflecting village traditional beliefs that the leaf monkeys are manifestations of dead people's spirits, the villagers do not shoot them. This has allowed their survival in an area of generally heavy hunting. During 90 minutes in the area in August 2010, three shots were heard, one within 100 m of the troop of monkeys; the animal under observation at that time looked briefly towards the shot, but did not flee. The monkeys were fully aware of the observers at 150–200 feet range, and at ease. A closer approach was impossible, however, suggesting that attempts are sometimes made on them by catapult. The villagers reported to Steinmetz and Baird (1997) that they restricted their own use of resources to ensure that food and habitat remained for the monkeys.

It is possible that neighboring villages also extend such protection to leaf monkeys, but the extent to which this is protecting a viable population, rather than a few troops (so far, confirmed only one) near villages is not known. Similar reverence for gibbons is known from various villages in Lao PDR, but traditional beliefs are weakening and some villagers themselves point out that the beliefs give gibbons no long-term security, particularly because outsiders (settlers or itinerant hunters) usually do not share them (Duckworth 2008). It is likely that the same is true for areas in Lao PDR where *T. germaini* is currently revered.

Timmins (2009) concluded that the Indochinese silvered leaf monkey (alone among primates there, including red-shanked douc and a form of gibbon) had been extirpated from surveyed parts of Houay Pen PFA by overhunting. This may be an increasingly common situation in encroached and fragmented areas. Substantial areas (that is, blocks exceeding 500 km^2) of forest on level or gentle lowland terrain and without a wide spread of villages across them survive in the species' Lao range only in few places. Based on current patterns of habitat extent and connectivity, human settlement and access routes, the areas that may stand the best chance of conserving large contiguous populations of the species in Lao PDR are the hilly lowlands south of the Xe Kong, parts of which are within Nam Ghong Provincial Protected Area; the lava soils between Dong Hua Sao NPA, Xe Pian NPA and the

Bolaven plateau, and Dong Khanthung pNPA (Fig. 1). These lowland southern landscapes are already identified as nationally very high conservation priorities for a suite of hunting-sensitive birds and mammals (Duckworth *et al*. 2005 and references therein). The Indochinese silvered leaf monkey should be added to the list of focal species for conservation in these areas, and given high priority in management plans and interventions.

The leaf monkeys of Ban Vangsikeo came to outsiders' notice during assessment of ecotourism possibilities in Savannakhet province, and have since then been promoted by the provincial authorities as a tourist attraction, with some revenues going to the village (P. Chanxaiyavong verbally 2010, J. Johnston verbally 2010). In principle, applying a solid financial value to living monkeys could ease the inevitable crisis when village customary beliefs weaken, but tourism money alone may not secure their future, based on Brown's (2009) findings that it did not prevent rapid population decline of a small gibbon population in an area of North Lao PDR.

Setting the Lao populations in an international context is hindered by the lack of clarity on the number of species involved and their relative distributions (both in and outside Lao PDR). Cambodia supports the largest numbers of *T. germaini* (*sensu lato*) globally; it is still widespread and numerous in some areas, especially the north-east and, perhaps, the lowland fringes of the Cardamom mountains in the south-west (Timmins and Ou 2001; Nadler *et al*. 2005; Timmins 2008; Coudrat *et al*. in press; Moody *et al*. in prep.). Populations in Vietnam and Thailand may be comparable to, or lower than, those in Lao PDR; in both countries, it apparently occurs now only as localized small populations (Nadler *et al*. 2003, 2005, 2007; Nabhitabhata and Cha-nard 2005).

If there are two Indochinese species of silvered leaf monkeys, Lao PDR may contain both. If the Mekong has significant bearing on their distribution, most of the Lao range will hold the eastern taxon, which globally may be extremely rare, and seriously threatened outside the Cambodian parts of its range. The small part of South Lao PDR west of the Mekong has no national protected area and monkeys there are probably now highly threatened (see discussion for pileated gibbon *Hylobates pileatus* in Duckworth 2008). Future wildlife and conservation surveys in Lao PDR south of 18°N should make every effort to assess gray leaf monkeys' status and to identify the form(s) present in each area. Rather little suitable survey (that based on species-focused direct diurnal observation) has occurred in southern Lao PDR in the 2000s (Duckworth 2008), so the present Lao status of the Indochinese silvered leaf monkey is unclear. That records from only one site after 2000 were traced here suggests that it may now be very rare. In this light, a critical analysis of the current status and future prospects of this monkey in Dong Phou Vieng NPA, paying particular attention to local beliefs (number of villages where cultural protection is strong, number of troops so protected, outlook for such beliefs) and to the government-administered tourism scheme, is urgently required. This is probably more important than investing resources in clarifying the overall present status of these monkeys in Lao PDR, because time may be very short to ensure the Dong Phou Vieng NPA population's survival. Besides, the challenges operating at any other sites in the country which do hold these monkeys may be insuperable in the time available.

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Appendix: site accounts

Dong Phou Vieng NPA: a group of at least eight, including one half-length youngster, was seen on 30 August 2010, 15 minutes' walk from Ban Vangsikeo (16°23'N, 106°02'E; 140 m; local name Ban Vongsikeo), in the patches and strips of semi-evergreen forest amid deciduous forest crossed by many small streams, at least one wide enough to break the canopy. Gray leaf monkeys were also seen here, within 20 minutes of entering the forest (locally called "Dong Sakee Sacred Forest"), on five of eight visits between December 1999 and June 2004 (J. Johnston *in litt*. 2010) and on 6 November 2007 (D. Van Gansberghe *in litt*. 2007). Most recently, in early 2011, J. Johnston (*in litt*. 2011) saw a single group estimated to comprise *c*.40 animals (including at least three golden infants) in this forest. At all four villages in the NPA interviewed in a 1997 survey, *taloung* was reported to be severely depleted, but less so in Ban Vangsikeo where numbers were assessed as half of those 10–30 years previously; the other villages estimated the current population to be, respectively, only 20%, 10% and 5% of earlier (Steinmetz and Baird 1997). S. Thonongto, the observer of direct sightings of silvered leaf monkey in the NPA given in Steinmetz (1998) reported (verbally 2010) that he saw the animals (twice) so poorly that although they were certainly colobines, even douc could not be ruled out; the identification was an assumption based on range in Thailand.

Xe Bang-Nouan NPA: one on Phou Satung in semi-evergreen forest (amid a landscape at the extreme dry end of the spectrum of semi-evergreen, widely verging on mixed deciduous) of the central hills (15°53'N, 105°53'E; 550 m) on 15 June 1994, several kilometers from the nearest large river (Evans *et al*. 2000, where altitude given in error as 650 m; RJT).

Dong Hua Sao NPA: [two hunters along the Houay Takit (*c*.15°04'N, 106°01'E; 220 m, but within a few kilometers rising to 1,000 m) during 31 January – 6 February 1996 were carrying two colobine corpses without hair, which they called *taloung*; they indicated that they came from the nearby hills (Evans *et al*. 1996b). No parts were salvaged and the identification is kept provisional because red-shanked douc also occurs in this area]. RB watched a group totaling seven or more (including at least one adult male, two adult females, two adult-sized individuals and one juvenile) over 10:15–11:34 on 18 December 1997 near the Houay Touay-Gnai (14°59'40"N, 106°08'02"E; *c*.340 m) in lowland semi-evergreen forest, about 50 m from the Houay Haet when first found (Boonratana 1998a).

Bolaven Southwest proposed NPA (pNPA): three troops, of at least 20, *c*.15 and 25 animals, were seen south of Ban Nonghin and west of the Xe Pian in partly logged semi-evergreen forest centered on 14°50'N, 106°26'E (260 m) on 17 and 19 April 1995. Several kilometers from the nearest large river, all were within 300 m of waterbodies; two groups were seen drinking at pools (Nong Hoi and Nong Gnai) amid dense forest (Evans *et al*. 2000; TDE).

[*Dong Ampham NPA*: a gray leaf monkey was glimpsed in the tall canopy of old-growth semi-evergreen forest, near the east bank of the Xe Kaman (14°56'N, 107°08'E; *c*.170 m) *c*.4 km downstream of the Xe Kaman 1 dam site in January 1997; villagers reported that the animal, *taloung*, was scarce and rarely seen (Davidson *et al*. 1997).]

[*Nam Ghong Provincial Protected Area, Attapu province*: a small group of rapidly-fleeing animals believed to be gray leaf monkeys was seen in evergreen forest at *c*.14°30'N, 106°31'E (very roughly, *c*.100 m; in Cambodia according to the national boundary on the RDPL SGE 1: 100,000 map boundary (as followed for Fig. 1), but said by villagers at time of survey to be in Lao PDR) on 5 March 1998 (P. Fernando *in litt*. 2010). (This record was erroneously presented as confirmed in Duckworth *et al*. [1999], based on a draft interim survey report which referred in error to observations of the species in two survey sectors.)]

Xe Pian NPA: a group of at least eight was seen at the Houay Kua salt-lick (*c*.14°33'N, 106°14'E; 140 m) on 25 December 1992, an area of short, open, semi-evergreen forest well supplied with pools and *c*.1½ km from the nearest canopy-breaking stream. On 5 March 1993, two groups were seen along the Xe Pian upstream of its confluence with the Xe Khampho, one of *c*.20, 500 m up (west bank; 14°31'N, 106°21'E; 80 m), and one of at least five, several kilometers up (east bank; 14°31'N, 106°22'E; 80 m), the latter in highly degraded secondary riverside growth (Duckworth *et al*. 1994; TDE). Details on a fourth record from this survey cannot now be traced but it was assessed as valid at the time and came from the same area along the Xe Pian as did the other records. A leaf monkey skull, presumed this species, was found on a January–February 1997 survey along the Houay Kua (140 m) (M. F. Robinson *in litt*. 1999); there were no field sightings and while survey style (focus on signs rather than sightings, large field teams) was not optimal for these monkeys, they could at best have been rare in the areas surveyed. Village reports at that time suggested they were most common deep in the southern part of the main block of semi-evergreen forest (RS), a habitat association at variance with all individual records here traced. [Guides meeting R. Tizard (*in litt*. 1998) reportedly saw a small group of gray leaf monkeys near Ban Sompoy (14°34'N, 106°28'E, 80 m) on 2 March 1998.]. MKP, who never observed the species in the field on multiple forays into the NPA in 2000–2001, saw a young captive along the Xe Pian between Ban Phonsaat and its confluence with the Xe Khampho on 19 or 20 December 2000 (Fig. 2). It was held by a Vietnamese who said he had been at his river camp for a month already, and that he purchased the monkey from a passer-by. It is unlikely that anyone would take a young leaf monkey caught far afield into this stretch of river to sell, but highly plausible that they would be taking one caught in the general area out for sale. Over 31 May – 4 June 2005, Bezuijen (2006) undertook several days of boat-based river survey along the same rivers as providing the 1993–2000 records and did not find the species (M. R. Bezuijen *in litt*. 2010).

Dong Khanthung pNPA: [in 1996 at least one individual identified by guides as a gray leaf monkey was heard along the Houay Phak (*c*.14°10'N, 105°32'E, 100 m) on 14 August 1996 (W. G. Robichaud in ICF 1996).] A group of 7–11 was frequently encountered in gallery forest along the Houay Ongvin (=Houay Vian; *c*.14°12'N, 105°30'E; 110 m) in March–April 1997, and another group was found *c*.6 km further along the river (Wolstencroft 1998). [A skinned, dried carcass, with the tail removed, but thought to be this species, was seen hanging on a gibbet at a villager's house at Nong Soumhoung (14°17'N, 105°41'E; 110 m) on 27 February (Round 1998).]

Areas where monkeys plausibly this species have been reported by local people, but there are no field records: in Xonbouly Eld's Deer Sanctuary (Muang [= District of] Xonbouly, Savannakhet province) *taloung* was reported in June 2002 in the south (adjacent to Dong Sithouan Production Forest Area (PFA) and to the north-east, adjacent to Dong Kapho PFA (Vongkhamheng and Phirasack 2002); however, conservation staff of the Savannakhet Provincial Agriculture and Forestry Office reported (verbally) in August 2010 that they did not consider that this sanctuary still held *taloung*. In Dong Sithouan PFA itself, *taloung* was reported in January 2000 from 20 villages interviewed, nearly all specifying that it lived around Phou Mali (16°04'N, 105°55'E; rising to nearly 800 m) and Dong Aa Chien (immediately south of Phou Mali, mostly at 300–600 m) (Boonratana 2000; RB). In Houay Pen PFA, Xekong province, *taloung* was reported, from habitats that resemble known Lao sites, to have occurred in the past, but no recent sightings could be traced (Timmins 2009). In Nam Pa PFA, Attapu province, in early 2010, *taloung* was said to persist only in a few areas and now to be very rare (JWD). All the foregoing are predominantly, or contain, extensive lowland areas. In Xe Sap NPA, *taloung*, described as gray and long-tailed, was reported by several villages around the southern border in early 1998 (Showler *et al*. 1998) and a gray leaf monkey (no local name noted) was reported around the Phou Leng area (southwest corner of the NPA, in areas at 560–1,080 m; big streams but no fringing tall forest) in early 1999, when some informants said it had become locally extinct in the past decade, some that it had declined dramatically. People from the other three parts of the NPA interviewed either knew of no such animal, or knew it and said it had always been absent from their area (Steinmetz *et al*. 1999). All the foregoing areas are south of Dong Phou Vieng NPA. In addition, Boonratana (1998b) received local reports in Phou Xang He NPA, some 50 km north of Ban Vangsikeo (Dong Phou Vieng NPA; the northernmost confirmed Lao locality for the species), that he attributed to the species. Neither his survey nor an earlier one (Duckworth *et al*. 1994) resulted in any records of this species, although unidentified leaf monkeys are apparently present (Duckworth *et al*. 2010).

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Note added in proof. M. R. Bezuijen (*in litt.* 2011) pointed out that one early explorer's text refers to *T. germaini* along the Lao-Thai Mekong, although without specifying which bank the animals were on: Garnier (1885: p.218) wrote "while we proceeded [by boat, upstream] beside the [Mekong] bank, a band of small, bizarrely colored monkeys descended from branch to branch to the ground and amused us with their skipping and gamboling. They have gray fur and black faces; a long white beard runs from one ear to the other." This sighting took place some way (probably within one or two days' non-mechanical boat-ride) upstream of the Khemmarat rapids (16°02'N, 105°13'E; 150 m above sea level), in the late 1860s. Garnier wrote that "above these last rapids the river [Mekong] becomes magnificent again. It runs, two thousand meters wide, in a vast plain...", and the monkeys were seen some way into this stretch, perhaps about 20–30 km north of Khemmarat. The topography is perfectly comparable to the confirmed Lao localities. The morphological description fits *T. germaini* very well; the only other taxon it could suggest is the form of François'-group leaf monkey *T. (f.) laotum*, but this is almost impossible on habitat grounds. The (imprecise) location may be similar in latitude to the northernmost confirmed Lao record.

Reference:

Garnier, F. 1885. *Further Travels in Laos and in Yunnan. The Mekong Exploration Commission report (1866–1868)*, vol. 2. Translated by W. E. J. Tips (1996) from original excerpts published in various issues of *Le Tour du Monde* 1869–1871 and in F. Garnier (1885. *Voyage d'Exploration en Indo-Chine*. Hachette & Cie, Paris). White Lotus Press, Bangkok, Thailand.

These three images show a single Indochinese Silvered Leaf Monkey *Trachypithecus germaini* in the spirit forest Dong Sakee near the village of Ban Vangsikeo, Dong Phou Vieng National Protected Area, Lao PDR, on 8 April 2012. This individual shows well the characteristics of the form '*margarita*', as described in the text. The variation in prominence of some key characters (such as the pale eye-rings) with lighting underlines the difficulties of accurate description of morphology through field sightings, especially given that their shyness means the monkeys are usually seen only briefly, at some distance, in motion and partly obscured. Of considerable concern is that since the last observations (2010) documented in the text, these formerly confiding monkeys have become much more shy: this was the only animal, in two groups seen on that visit, that could be approached within 100 m. Ongoing illegal extraction is severe at the site; many non-local people are involved, who do not share the reverence for this monkey typical of that traditionally shown by residents of Ban Vangsikeo. Thus, the outlook for this population remains bleak. Photographs by Jonathan C. Eames.

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The Conservation Status of Phayre's Leaf Monkey *Trachypithecus phayrei* in Lao PDR

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Abstract: Phayre's leaf monkey *Trachypithecus phayrei* had fewer confirmed 1990s records in Lao PDR than any other monkey known from the country, suggesting a general rarity there. This review collates records, historical and recent, to evaluate its national conservation status. Although in no area have surveyors regularly and readily seen the species, records come from a wide scatter of areas in and north/west of Nam Kading National Protected Area to the far north and west of the country. There are inconclusive indications of occurrence up to 120 km south of confirmed records, but this part of the country is well enough surveyed that the animal must be very rare there, if it occurs at all. Much of North Lao PDR comprises rugged highlands over 800 m altitude, but only one Phayre's leaf monkey field record is from above this height (at 1,125 m). Whether this apparent altitudinal restriction is a natural pattern or reflects heavy hunting is unclear. Despite their lower-lying locations, records are not associated with gentle terrain. Most records come from forest with a heavily broken canopy and much tall bamboo; none is from deep within extensive closed-canopy forest. This might simply reflect the paucity of such forest within the known Lao geographic and altitudinal range, but a genuine habitat association with broken canopy and tall bamboo is likely. The status of Phayre's leaf monkey in Lao PDR is less grim than was feared a decade ago, and it inhabits three national protected areas, which are benefitting from long-term external collaboration. Nonetheless, its status in Lao PDR cannot yet be considered secure. Lao populations are probably relatively insignificant to the global status of *T. phayrei* as here taxonomically constituted.

Key Words: conservation, distribution, geographic range, habitat, Laos, Phayre's langur, *Semnopithecus holotephreus*, *Trachypithecus crepusculus*

Introduction

Lao People's Democratic Republic (Lao PDR; Laos) is an inland country of 236,800 km² in South-east Asia, retaining a high proportion of natural and semi-natural habitats relative to most of its neighbors, and thus of high global conservation significance (for example, Thewlis *et al*. 1998). In a comprehensive review of the national status of the mammals of the country, Duckworth *et al*. (1999) found that Phayre's leaf monkey *Trachypithecus phayrei* had fewer confirmed recent (post-1988) records than did any other Lao monkey, despite its fairly wide Lao range. Similarly, Nadler *et al*. (2003) traced rather few reliable recent records from Vietnam, and considered it nationally to warrant the IUCN Red List category of Critically Endangered. Hunting, including of monkeys, is intense in these two countries (for example, Duckworth *et al*. 1999; Nadler *et al*. 2003), bringing some colobines to the brink of extinction (for example, Stenke and Chu 2004). Globally, Phayre's leaf monkey is categorized as Endangered by *The IUCN Red List of Threatened Species* (Bleisch *et al*. 2008). Here we review its conservation status in Lao PDR.

Throughout most of the latter half of the twentieth century, the gray leaf monkeys of northern Lao PDR were generally treated, with those of parts of Vietnam, Thailand, Yunnan province of China, and Myanmar, as a single taxon, *crespusculus* (type locality: Mount Muleiyit, Myanmar), conspecific with *T. phayrei* (type locality: Arakan, Myanmar), itself placed in various genera (*Trachypithecus*, *Semnopithecus* or *Presbytis*) and ranging into north-east India south of the Brahmaputra (Srivastava 2006). However, Brandon-Jones *et al*. (2004) chose a radically different system (earlier presented in Brandon-Jones [1984], but with minimal discussion), considering *crepusculus* a junior synonym of *holotephreus*, which taxon they treated as a race of *T. barbei*, placing *phayrei* as a race of dusky leaf monkey *T. obscurus*. This has not generally been followed, with, for example, Groves (2001, 2005) recognizing a fairly conventional *T. phayrei*, with *crepusculus* a constituent race.

Liedigk *et al*. (2009) proposed that *crepusculus* was so distinct that it would be best regarded as a full species, indeed as a distinct species-group within *Trachypithecus*. However, this was based only on mitochondrial DNA, on which character the analyzed animal(s) were more similar to François'-group leaf monkeys *T. francoisi* (*sensu lato*) than to *T. obscurus*, the oldest name in the species-group to which *T. phayrei* is generally seen to belong on morphological grounds (for example, Groves 2001). Based on morphology and nuclear DNA, Liedigk *et al*. (2009) considered *crepusculus* a typical member of the *T. obscurus* species-group, a result in conflict with that from mitochondrial DNA. Comparable cases in mammals of discordance between mitochondrial phylogeny versus nuclear phylogeny and morphology (for example, banteng *Bos javanicus*; Hassanin and Ropiquet 2007) have not resulted in proposals for segregation at species level. Furthermore, because other forms of *T. phayrei* were not included in the analysis, the reason to consider *crepusculus* highly distinct from *phayrei* itself, rather than, for example, both of them well separated from *T. obscurus*, is not apparent. Moreover, Liedigk *et al*. (2009) did not state the number or wild origin of *crepusculus* tested, but given that it or they came from the Endangered Primate Rescue Center (Cuc Phuong National Park, Vietnam), it seems likely to have been Vietnam. There is no particular reason to assume that *crepusculus* from the type locality (close to the western extent of its range, in Myanmar, and separated by several major rivers from northern Vietnam, and thus from the entire range of *T. francoisi* [*s.l.*]) would carry the same mtDNA as Vietnamese animals. Indeed, Wang *et al*. (1997) found surprisingly high mtDNA variation within the two animals they analyzed and identified as *T. phayrei* (no subspecies identification given) from Yunnan (Xishuangbanna and Hekou). Roos *et al*. (2007), using the preliminary results of Liedigk *et al*. (2009), already treated *crepusculus* as a distinct species, but excluded Myanmar from its range. Amid all this uncertainty, however, one fixed point is that *crepusculus* refers to the animals at Mount Muleiyit in Myanmar, and if those in Vietnam and perhaps other countries to the east are considered different, then (as pointed out by Pocock [1935]), they need another name. Thus, considerably more investigation is needed before the merits and application of the proposal of Liedigk *et al*. (2009) can be assessed, and here we continue to treat *crepusculus* as a race of Phayre's leaf monkey, reflecting the taxonomic treatment of *The IUCN Red List of Threatened Species* (Bleisch *et al*. 2008).

Conventions concerning locations

Areas and sites referred to in the text are marked on Figure 1. Place names are based on the 1985–1987 series of 1:100,000 maps of the RDP Lao Service Géographique d'État (RDPL SGE) maps with the minor modifications of Thewlis *et al*. (1998), except that the Nakai plateau and derivatives are spelled thus, not as Nakay, reflecting widespread current usage. Where there is no RDPL SGE map-name, the name in local usage is given, transliterated according to the original observer. Coordinates and altitudes, except where stated, are derived from the RDPL SGE maps. Considerable detail accompanies the distributional data, following the urging of Brockelman and Ali (1987) for such precision in primate records. Habitat types mostly follow those of the original source with no attempt to convert all into one classification system, because no such system is yet in wide use for the country (Rundel 2009).

Lao words incorporated in place-names: *Ban* = village (here, meaning the area surrounding the village, rather than the village itself); *Houay* = stream; *Muang* = administrative district of; *Nam* = river; *Pak* = river mouth; *Phou* = mountain or hill; *Sop* = river mouth; *Xe* = river.

Table 1. Historical (pre-1980) records of Phayre's leaf monkey from Lao PDR¹.

Site collected	Approximate location	Date	Collection and number	References
Ban Muangyo	21°31'N, 102°51'E	14 May 1929	FMNH 31757	Osgood 1932; Fooden (1976)
"	"	16 May 1929	FMNH 31758	"
"	"	15 May 1929	FMNH 31759	"
"	"	16 May 1929	FMNH 32546	"
Nam Ou, Ban Muangngoi – Louangphabang²	20°30'N, 102°30'E	21 May 1929	FMNH 31756	"
Xiangkhouang²	19°20'N, 103°22'E	8 Jan 1926	BMNH 1926.10.4.6	Thomas (1927); Fooden (1976); Napier (1985)
Ban Nale²	18°42'N, 101°34'E	1861	BMNH 1861.10.8.1	Brandon-Jones (1995)
Mekong forests 30 km upstream of Vientiane²	18°01'N, 102°24'E	Between 1963–1972	None	³Deuve (1972)
Khet Dong Hieng	17°53'N, 101°34'E	31 Jan 1920	ZRCS 4-546	Fooden (1976), Weitzel *et al*. (1988)

[1] Delacour (1940), followed by Duckworth *et al*. (1999), also listed "Muong Mo" as a Lao locality for this species; however, this is in Vietnam (Osgood 1932).

[2] Not safely assumable as originating particularly near the co-ordinates given, particularly for Ban Nale, which is only an inferred locality (Brandon-Jones 1995; Duckworth in press).

[3] Deuve (1972) has many elementary errors (for example, Duckworth *et al*. 2010), but this record seems reliable because the physical characters (bold white around the mouth, and pale gray around the eyes) of a single specimen from a specific locality were described. The date range is derived through the species not having been included in Deuve and Deuve (1963).

FMNH = Field Museum of Natural History, Chicago; BMNH = British Museum (Natural History); ZRCS = Zoological Reference Collection, Raffles Museum for Biodiversity Research, Singapore.

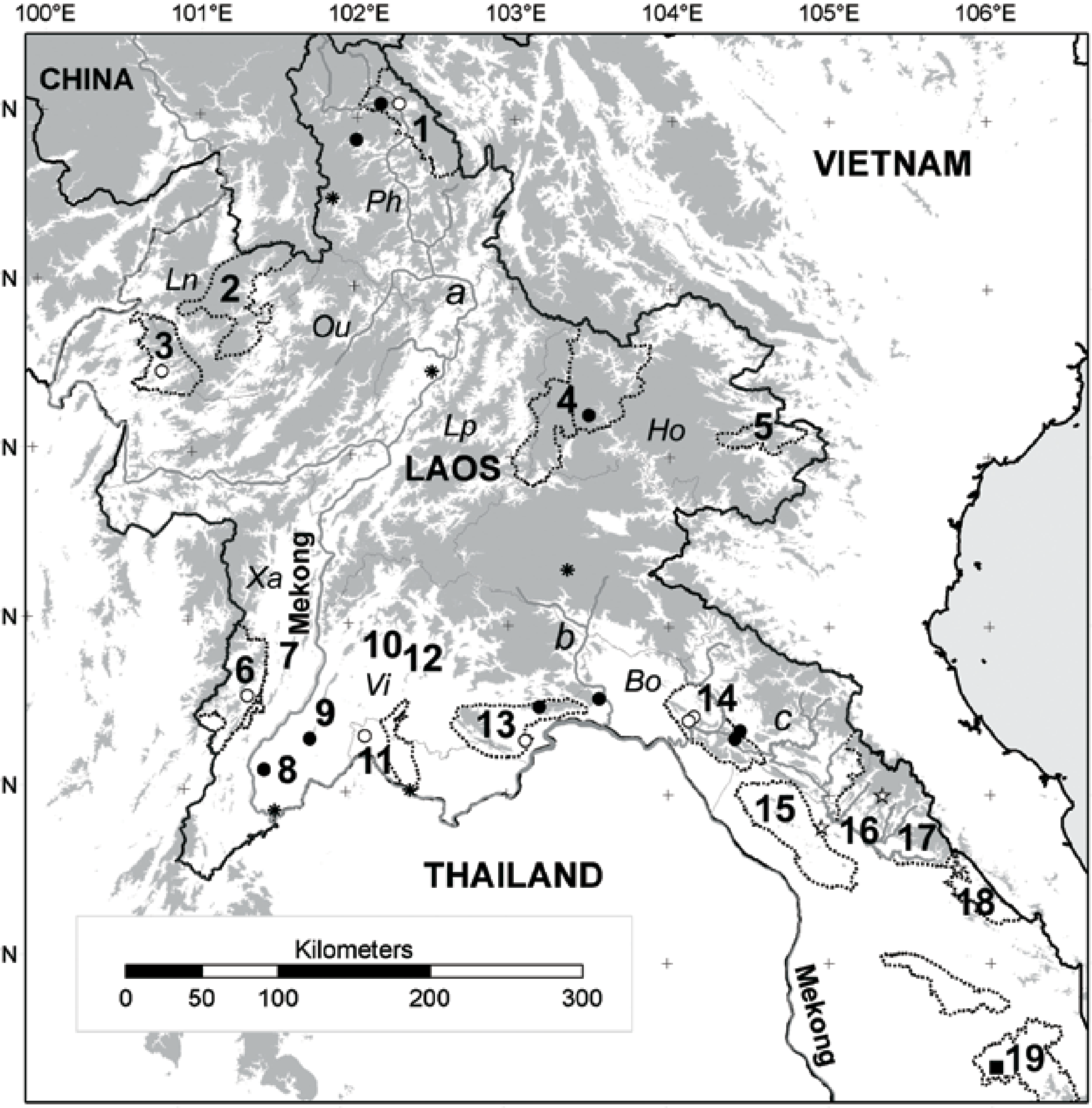

Figure 1. Lao PDR, showing localities mentioned in the text and records. Background shading shows land over 800 m. All national protected areas (NPAs) in the area covered are shown, but only those national production forest areas (PFAs), provinces, districts and rivers referred to in the text, are shown.

● Modern record of Phayre's leaf monkey, identification confirmed

○ Modern record of Phayre's leaf monkey, identification provisional

☆ Modern report of leaf monkey potentially Phayre's leaf monkey, south of known range of the latter

* Historical record of Phayre's Leaf Monkey, identity confirmed, locality imprecise

■ Northernmost record of Indochinese silvered leaf monkey in Lao PDR

Provinces: *Bo* = Bolikhamxai; *Ho* = Houaphan; *Ln* = Louang-Namtha; *Lp* = Louangphabang; *Ou* = Oudomxai; *Ph* = Phongsali; *Vi* = Vientiane; *Xa* = Xaignabouli.
Rivers: *a* = Nam Ou; *b* = Nam Ngiap; *c* = Nam Kading

Numbered areas: 1 = Phou Dendin NPA; 2 = Nam Ha NPA; 3 = Nam Kan NPA; 4 = Nam Et–Phou Louey NPA; 5 = Nam Xam NPA; 6 = Nam Pouy NPA; 7 = Phou Phadam PFA; 8 = Muang Sanakham, Vientiane province; 9 = Phou Gnouey PFA; 10 = Nongpet–Naxeng PFA; 11 = Muang Sangthong, Vientiane municipality; 12 = Muang Vangviang, Vientiane province; 13 = Phou Khaokhoay NPA; 14 = Nam Kading NPA; 15 = Phou Hinpoun NPA; 16 = Nakai plateau; 17 = Nakai–Nam Theun NPA; 18 = Hin Namno NPA; 19 = Dong Phou Vieng NPA

Methods

Many site-focused, direct-observation mammal surveys were undertaken across Lao PDR during 1992–2007, with survey effort characterized by Timmins and Duckworth (1999, 2008) citing the original, often internal, reports from each. Most consisted of a few weeks to a few months to assess general habitat type and condition, and to seek by direct observation (mostly during daylight) birds and large mammals (generally, those identifiable without the need for specimen procurement) of elevated national and, especially, global conservation concern. Monkeys were thus among the best covered groups of mammals. Results from these surveys were supplemented by the authors' own surveys in 2008–2010, and by enquiries for Lao records of the species from other wildlife surveyors.

Objective identification of Lao sightings of gray leaf monkeys as Phayre's leaf monkey needs care, because another gray species, Indochinese silvered leaf monkey *T. germaini* (also of disputed taxonomy), inhabits the country. There are too few Lao specimens of gray leaf monkeys to define even the coarse ranges of both these species (Table 1; also, Timmins *et al*. 2011). Although the two are readily separated with good views and careful observation, monkeys recorded during 1990s–2000s surveys in Lao PDR were typically shy, so views were often brief and partly obscured. Identification of all field records from these decades has, therefore, been checked during preparation of this review. Hamada *et al*. (2007: p.166) stated that Phayre's leaf monkey has an "insignificant pale colored "ring" around the eyes": this is incorrect, the ring being very bold in Lao animals (Figs. 2 and 5; also Duckworth *et al*. 1999: Plate 13), as reported by Francis (2008) for *crepusculus* throughout its range, and as portrayed for presumed Vietnamese animals in Geissmann *et al*. (2004) and Liedigk *et al*. (2009). However, Indochinese silvered leaf monkeys can have noticeable pale spectacles (Nadler *et al*. 2005; Timmins *et al*. 2011: Fig. 2), and the degree of overlap in strength with Phayre's is unknown (but may well be negligible). More importantly, the two differ greatly in the form of long hair tufts on the head, and the contrast in pelage tone across the body, particularly the limbs with the torso.

Reliable objective identification to species using local name is impossible with this species in Lao PDR. Echoing similar problems elsewhere (Choudhury 1988; Nadler *et al*. 2005), Duckworth *et al*. (2010) and Timmins *et al*. (2011) discussed the difficulties of this activity with colobines in Lao PDR. The name *khang* in wide use in the northern half of Lao PDR is commonly associated with this species, but is probably best seen as meaning simply *Trachypithecus*: towards the south of its area of common use, in Bolikhamxai province, it may well be used for François'-group leaf monkey and, reflecting Thai influence, it may at least occasionally be used for any leaf monkey right to the south of the country (Timmins *et al*. 2011). *Khang* needs careful distinction from *kang*, used for macaques *Macaca*, usually as *ling kang* (Duckworth *et al*. 2010). Questioning of rural people with pictures to try and determine species of leaf monkey present seems essentially a waste of time, with both Hansel *et al.* (1998b) and Hamada *et al*. (2007) finding that villagers in the Lao northern highlands generally selected silvered leaf monkey, not Phayre's, as the species present. They are unlikely to be correct, given the locations of the available Lao specimens and direct sightings for the genus as found here and by Timmins *et al*. (2011). Moreover, animals camera-trapped in the general area of reports to Hansel *et al*. (1998b) are typical Phayre's leaf monkeys in appearance (Fig. 2), as is the single specimen from nearby Xiangkhouang.

Figure 2. Phayre's leaf monkeys *Trachypithecus phayrei* at a mineral lick in Nam Et–Phou Louey National Protected Area, Lao PDR, 18 January 2005. (above) two animals resting; (below) one animal eating or drinking. Photographs by camera-trap operated by Nam Et–Phou Louey National Protected Area and WCS Lao Program.

Records

Historical (pre-1980) records from Lao PDR are presented in Table 1. Modern records come from ten areas (seven confirmed and three provisional—the latter enclosed in square brackets), with imprecise village reports from various others.

Phou Dendin National Protected Area (= NPA). A group of at least six was seen along the Nam Ou in streamside forest between the mouths of the Nam Khang and Nam Toho (very roughly, 22°05'N, 102°09'E; 560 m) on 1 June 1995 (Evans *et al*. 2000; WGR). [A troop of 5–7 gray leaf monkeys was seen briefly, in the relatively mature riparian forest downstream of

Ban Sopkhang, at 22°05'N, 102°16'E (560 m) on 17 March 2005 (Ruedi and Kirsch 2005). Interviews in 2004–2005 received widespread reports of gray, long-tailed, monkeys (as *khang* or *kang*: not noted which) persisting in the NPA (Duckworth *et al*. 2005b).]

Western Phongsali province. Along the Nam Ngay (21°52'N, 102°00'E; *c*.800 m) on 27 March 1996, a local guide shot and killed (after the animal fell, wounded, from the canopy) a male among a troop, in little-degraded semi-evergreen forest on a ridge above the river (Duckworth *et al*. 1999: Plate 13; WGR).

[*Nam Kan NPA*. In March 2010, J.-F. Reumaux (verbally to Robichaud *et al*. 2010) reported that a troop of 30 gray leaf monkeys is regularly seen at the tourist resort 'The Gibbon Experience' (20°28'21"N, 100°48'03"E, taken from Google Earth; altitude *c*.550 m) in fairly evergreen forest, degraded in places and near a river; villagers reported gray leaf monkeys, as *khang* in Lao, *xang* in Khmu, widely, suggesting they may be locally common in some parts of the NPA (Robichaud *et al*. 2010).]

Nam Et–Phou Louey NPA. During an intensive camera-trap program (Johnson *et al*. 2009), Phayre's leaf monkey was recorded at only one site (A. Johnson *in litt*. 2010), a mineral lick at 20°15'04"N, 103°29'31"E (taken from a GPS under WGS84 datum), at 1,125 m altitude, in a large rugged highland area. The mineral lick lies in montane forest with a broken canopy that reflects several episodes of cutting (S. Saysinghan and A. Johnson *in litt*. 2010); it is 6 km from the nearest land below 800 m, this being the narrow (800 m contours less than 1 km apart) Nam Neun valley dropping to 640 m locally. Photographs were taken 11 times between 08:10 and 13:34 on 18 January, thrice between 09:20 and 11:00 on 20 January, and at 12:25 on 4 February 2005 (Fig. 2). Hansel *et al*. (1998b) received village reports noted as of *kang* (but perhaps a transcription of *khang*) which apparently referred to gray leaf monkeys from several parts of the NPA. Since 2003, extensive conservation management activities, notably anti-poaching patrols, have generated very few reports of leaf monkeys (A. Johnson *in litt*. 2010), suggesting that they are rare or at best very localized in the NPA; consistent with this, a lengthy direct observation survey in the NPA in 1998 (Davidson 1998) did not observe the genus.

[*Nam Pouy NPA*. Boonratana (1997) reported observing three groups of Phayre's leaf monkey in this NPA in a short survey in 1997. However, two referred to village reports, and the other was not seen well enough for certain identification to species (R. Boonratana *in litt*. 2011): a group of at least 3–4, on 3 May 1997 when flushed in mixed deciduous forest on a ridge near to 18°33'30"N, 101°23'20"E (within 400–550 m asl). That any gray leaf monkey in this area can safely be assumed to be Phayre's on the basis of range is confounded by Boonratana (1998), who observed a group of what he identified as silvered leaf monkeys in the same protected area in 1998 (detailed in Timmins *et al*. 2011); unfortunately no notes were taken of identification, and identity of leaf monkeys here should best be left unresolved.]

Muang Sanakham, Vientiane province. A skin and head (Fig. 3) were seen at a hunters' camp beside the Houay Oum (18°07'20"N, 101°29'50"E; *c*.300 m) amid hills supporting extensive tall bamboo and riverine forest (Fig. 4) on 30 October 2000 (Hansel 2004, where the record was dated erroneously as 2004 in Table 1); the skull and a photograph of the skin were sent to the Natural History Museum, London, UK (registration number BMNH 2010.310). Although skulls are difficult to identify objectively to species (Pocock 1935), the overall gray color of the skin, especially of the tail, suggests *T. p. crepusculus* (D. Brandon- Jones *in litt*. 2011). A group of six (five adults and one young molting from orange to gray pelage) was seen in tall bamboo and secondary growth with remnant tall trees from semi-evergreen forest at Kok Kawdinpang (18°18'05"N, 101°46'49"E, taken from a GPS under WGS84 datum; *c*.500 m), east of Ban Phonsavat, in Phou Gnouey Production Forest Area (= PFA) on 6 April 2010 (Suford in press). Villagers reported near-daily

Figure 3. The head of a hunted Phayre's leaf monkey *Trachypithecus phayrei*, being cooked as part of professional hunters' haul of mixed wildlife. Muang Sanakham, Vientiane province, Lao PDR, 30 October 2000. Photograph by T. E. Hansel.

Figure 4. Typical tall bamboo habitat of Phayre's leaf monkey *Trachypithecus phayrei*, Muang Sanakham, Vientiane province, Lao PDR, October 2000. Photograph by T. E. Hansel.

sightings of *khang* in the same general area, during the survey, and said that scattered populations persisted across the region, including on large karsts west of the village (and outside the PFA).

[*Muang Sangthong, Vientiane municipality*. The fresh headless skin and skull of a gray leaf monkey, called *khang* (or *kang*), were seen along the Nam Sang (*c*.18°20'N, 102°07'E; 200 m) several kilometers upstream of Ban So, on 16 February 1996; the hunter said that he had shot it on 15 February from a group of about six, in logged streamside forest with much tall bamboo. Identification as Phayre's leaf monkey is provisional, based on range. *Khang/kang* was reported in various villages to remain locally common in the area (Duckworth 1996; JWD).]

Phou Khaokhoay NPA. A troop of *c*.20 was watched along the Nam Mang valley bottom forest, with extensive tall bamboo (18°31'N, 103°12'E; 260 m) on 9 November 1994 (Evans *et al*. 2000; JWD). [Two gray leaf monkeys were seen in a valley bottom around the Houay Namhi (very roughly, 18°19'N, 103°07'E; 250 m) one day during 5–10 September 1994 (Payne *et al*. 1995).] Both points of sighting contained more tall trees and a more contiguous canopy than many nearby areas of this generally broken-canopied landscape which had until the early 1990s been part of State Forest Enterprise 3.

Lower Nam Ngiap catchment. A shot animal (from a group of at least five) was photographed (Fig. 5) *c*.11 km north-west of Ban Namngiap, at 18°34'09"N, 103°34'25"E (taken from Google Earth; within 340–450 m asl) in rugged terrain with broken forest, within 200 m of a stream on 17 February 1999 (S. Watson *in litt*. 1999, 2010).

Nam Kading NPA. A group of about six was seen in degraded semi-evergreen forest and on adjacent karst north of the Nam Xouang (18°23'N, 104°27'E; 350 m) on 27 April 1995, and a single animal was seen in semi-evergreen forest with very uneven canopy and extensive bamboo on the south slope of Phou Ao (18°20'N, 104°25'E; 500 m) on 29 April 1995 (Evans *et al*. 2000; RJT). [In 2005, two sightings of gray leaf monkeys in the north-west sector of the NPA, north and west of the Nam Kading–Nam Mouan were, on the basis of range, presumably Phayre's (Timmins and Robichaud 2005): on 6 February at 18°27'54"N, 104°09'45"E (at or below *c*.500 m), and on 7 February at 18°26'26"N, 104°07'50"E (*c*.350 m). This area has very heterogeneous vegetation, with lots of tall straight smooth-culmed bamboo, sprawling bamboo, vines, and a very uneven, often very low, canopy, or no real canopy at all, and patches of tall forest (RJT).]

Areas where animals presumably this species have been reported by local people but there are no field records

Monkeys consistent in the stated morphology with gray leaf monkeys, and assumed to be Phayre's leaf monkey on range, have been reported during village interviews in the northern highlands in at least Nam Ha NPA (Johnson *et al*. 2003); Nam Xam NPA (Hansel *et al*. 1998a); Divisions 3 and 7 (in Xaignabouli and Vientiane provinces respectively) of the Hypa concession (HFI 1999); Phou Phadam PFA, Xaignabouli province (Suford in press); Nongpet–Naxeng PFA, Vientiane province (Suford in press); Muang Vangviang (Duckworth in press); and at 23 of 46 sites on a 1,450 km drive through Houaphan, Louangphabang, Oudomxai, Louang-Namtha and Phongsali provinces during 22–31 May 2006 by Hamada *et al*. (2007). The reports vary in their efforts to minimize problematic factors which confound their reliability and are listed for completeness, even including those with minimal safeguards in methodology.

Habitat Use

No Lao Phayre's leaf monkey record with habitat information comes from deep within extensive closed-canopy forest. Instead, records are from forests with broken canopy and extensive tall bamboo, such features perhaps resulting from human land-use ancient or recent, underlain by geological

Figure 5. Recently shot Phayre's leaf monkey *Trachypithecus phayrei*, Lower Nam Ngiap catchment, Lao PDR, 17 February 1999. Photographs by S. Watson / RMR.

and climatic factors. The tall bamboo noted at many sites is a single structural type (perhaps even a single species): tall, weakly clumped with large gaps between clumps, stems dominating the ground layer vegetation, stems with little lower branching, and the stems reaching what would be sub-canopy, but the bamboo itself often forms the canopy because it is growing in areas with only sparse big trees overtopping it (Fig. 4). Various observations from India and Myanmar stress the importance of shoots of tall bamboos (for example, *Melocanna*) in this leaf monkey's diet or at least the frequency with which monkeys are seen in such bamboo (for example, Green 1978, Mukherjee 1982, Choudhury 1994a, 1994b, Gupta and Kumar 1994, Raman 1996, Srivastava 1999, 2006, Platt *et al*. 2010). At least in Lao PDR, such bamboos seem to indicate past (sometimes perhaps ancient) cultivation and/or fire (a topic worthy of further investigation), and some of the Lao records are from areas with a very uneven canopy and heavy recent logging. Deeper analysis (which would require more records) might even find it to be more common in the latter than within closed-canopy tall forest. This use of degraded areas is well known for Phayre's leaf monkey in India and surrounds (Green 1978; Gupta and Kumar 1994; Raman 1996; Srivastava 1999, 2006), although information specific to *crepusculus* remains too scant to confirm its applicability to that taxon. The number of Lao records far from any canopy-breaking stream shows that the species is not strongly associated with such habitats, in apparent contrast to Indochinese silvered leaf monkey in southern Lao PDR (Timmins *et al*. 2011); the Lao Phayre's leaf monkey records from streamsides simply reflect the preponderance of survey effort along them.

One record came from limestone karst, in Nam Kading NPA, a habitat a little further south in Lao PDR supporting François'-group leaf monkeys (Duckworth *et al*. 2010). More generally, most records with precise locality were in hilly landscapes, but nearly all land within Phayre's leaf monkey's Lao range and on gentle terrain is converted to agriculture with remaining forest patches so small that hunting-sensitive species have been eradicated. Even the few larger tracts are too heavily used by people for the species's use of plains in Lao PDR to be evaluated. It is, however, certainly not tied to precipitous regions in the way that François'-group leaf monkeys in Lao PDR seem to be (Duckworth *et al*. 2010). Karst use has been reported from Thailand (Lekagul and McNeely 1977) and Vietnam (Nadler *et al*. 2007).

Altitudinal Range

Lao Phayre's leaf monkey records are not spread across the altitudes of the survey, but neither the true pattern nor the reason(s) behind it are clear. Various records came from altitudes as low as any in the general survey area in question (with the lowest at 260 m). The highest recorded altitudes were only 1,125 m, *c*.800 m and 560 m; and while precisely located records are too few to propose a typical upper limit in the country, the paucity of records from above 800 m suggests this monkey is not common in higher-lying areas. Direct-observation survey effort specifically in areas with Phayre's leaf monkey records has been too limited above *c*.800 m to speculate on altitude use in them, even in Phou Dendin NPA with the best coverage of higher altitudes (Fuchs *et al*. 2007). Discounting areas uninformative about leaf monkeys because habitat is so fragmented that they are likely to have been hunted out if they were ever present (for example, Duckworth *et al*. 2002; Duckworth in press), the considerable direct-observation survey effort within the general Lao range of this species over 800 m unfortunately comes mostly from several areas where Phayre's leaf monkey has not been found in the adjacent lower-lying forest either: Nam Et–Phou Louey, Nam Xam and Nam Ha NPAs (Tizard *et al*. 1997; Davidson 1998; Showler *et al*. 1998). None of these areas was well enough surveyed in lower-lying areas to comment on the species's likely status at such altitudes. Therefore, the lack of these surveys' records from above 800 m, while suggestive, is not strong evidence of altitudinal patterns: perhaps the species is simply not in those areas, or is very rare in them. The record at 1,125 m in Nam Et–Phou Louey NPA proves at least occasional occurrence well above 800 m, and, because the site is 6 km from any land below 800 m, it seems that some groups do live well above 800 m. The record was at a mineral lick, which Phayre's leaf monkeys will travel at least ½ km outside the usual group range to use (Pages *et al*. 2005), and in rugged terrain such diversion could take them well outside their normally occupied altitudinal range.

Historical records also suggest rarity at high altitude. In 1929, the Kelley–Roosevelts' expedition spent a fortnight each based at Ban Khomen (*c*.1,100 m; no land anywhere near lies below 800 m) and at Ban Muangyo (680 m) in Phongsali province (Bangs and Van Tyne 1931): in the former they collected no Phayre's leaf monkeys, but at the latter, four, and they collected a further one on their journey down the Nam Ou, probably also in the lowlands. While far from conclusive, this is consistent with this monkey being rare in Lao PDR over about 800 m altitude. Set against this, Lowe (1947: p.30) wrote that in December 1925 he saw grey leaf monkeys (presumably this species) some way east of Ban Nonghet (19°30'N 103°59'E), that is, just on the Vietnamese side of the Lao–Vietnam border, by the road through the forest apparently "at higher levels" (presumably well above 800 m); but the description of these sightings as "at times" on the journey gives some doubt as to whether they were specifically "at higher levels" or not. His team's specimen from Xiangkhouang, which lies at about 1,100 m, lacks precise information on the animal's origin, although it was evidently fresh when acquired, given the specimen tag notes on skin colors. The collecting team (under J. Delacour) acquired animals in local markets and were sometimes highly imprecise over locality (for example, Duckworth *et al*. 2005a): David-Beaulieu (1944) already pointed out (under his species account for Large Scimitar Babbler *Pomatorhinus hypoleucos*) that the altitude of (Ban) Xiangkhouang for some of the specimens to which Delacour assigned this locality was well above his own (very substantial field) experience with these species in this area.

The pattern of altitudinal records may reflect at least partly the effects of hunting on large quarry species. The surveys of Nam Ha, Nam Et–Phou Louey and Nam Xam NPAs, each of highlands within the known range of Phayre's leaf monkey but which did not record the species, all saw few or no macaques, gibbons *Nomascus*, black giant squirrel *Ratufa bicolor* and large hornbills (Bucerotidae), whereas some or most of these other hunted species of similar body size were found (although generally much less often than in similar habitats of southern Lao PDR) by broadly comparable surveys in each of several areas also with leaf monkey direct-sighting or field remains records: Phou Dendin NPA, Muang Sangthong, Phou Khaokhoay NPA and Nam Kading NPA (Duckworth 1996, 2008; Tizard *et al.* 1997; Davidson 1998; Showler *et al.* 1998; Thewlis *et al.* 1998; Duckworth *et al.* 2005b; Timmins and Robichaud 2005; Fuchs *et al.* 2007; Timmins and Duckworth 2008, in prep.). Another northern highland area with Phayre's leaf monkey records, Nam Kan NPA, has not had enough surveys to evaluate populations of these hunting-sensitive species, but retains anomalously many gibbons in a northern highland context (Geissmann 2007). Most significant is that the 1990s direct observation surveys of Nam Ha, Nam Et–Phou Louey and Nam Xam NPAs saw very few macaques (in total, eight sightings in 30 person-weeks; Timmins and Duckworth in prep.). Macaques were undoubtedly present in all areas, but were very shy, presumably through hunting. The 1990s surveys in Lao PDR outside the northern highlands recorded macaques far more frequently than they did leaf monkeys (Ruggeri and Timmins 1997), and this simple comparison suggests the possibility that leaf monkeys were present but overlooked in these three NPAs with a highland survey focus. There is certainly enough risk of this to prevent firm deductions about altitudinal usage by Phayre's leaf monkey in Lao PDR.

It is plausible that these two factors operate in combination, with higher altitudes providing suboptimal habitat and so hunting pressure, which is intense across all altitudes, has been more damaging to leaf monkeys there. The altitudinal distribution of the tall bamboo from which many Lao Phayre's leaf monkey records come seems not to have been documented; but from the authors' memories it may be scarce above 800–1,000 m, which suggests a possibility that the distribution of records across altitude in fact does reflect the real occurrence of the monkey. The observed pattern of altitudinal records in Lao PDR is consistent with observations in north-east India, with upper limits there stated to be about 800 m (Srivastava 1999) or 1,000 m (Choudhury 2001).

Distribution

Recent Lao records of Phayre's leaf monkey are all from the northern part of the country (Fig. 1). Their distribution polygon includes the historical locations (Table 1) except the most southwesterly record, the area around which has not been investigated recently. Nearly all records are close to the Mekong and its major tributaries, the Nam Ou and Nam Kading. This leaves the main northern highlands a large area conspicuous for the paucity of records: a historical specimen from the former town of Xiangkhouang, and a camera-trap location from Nam Et–Phou Louey NPA. There are two plausible, non-exclusive, reasons behind this pattern — altitude and hunting — but it is just possible that it is simply an artifact of survey coverage (see 'Altitudinal Range').

The direct sightings presented here extend the known range somewhat to the south-east of the specimens, although the record from furthest south remains that from the west of the country, from Khet Dong Hieng at 17°53'N. Three field sightings, from Phou Khaokhoay NPA in November 1994 and from Nam Kading NPA in April 1995 (Evans *et al*. 2000), involved prolonged, close views of the animals, and the detailed field notes confirm identification. There is no record of any gray leaf monkey in Lao PDR south-east of these localities until the silvered leaf monkeys in Dong Phou Vieng NPA (Timmins *et al*. 2011). From this large (*c*.300 km, north–south) record-less swathe come, however, some inconclusive indications of gray leaf monkeys.

Duckworth (1998) assigned provisionally, based on range, to Phayre's leaf monkey two animals seen along the Navang logging road (Nakai–Nam Theun NPA; *c*.18°00'N, 105°20'E) in 1996; neither facial pattern nor crest characters were visible (N. L. Ruggeri verbally 1996). François'-group leaf monkey was not considered in the 1996 identification at the time because there is no karst anywhere near the sighting location; however, in 1999 that species was found far from karst within the NPA, and there are now various other non-karst records from further south in Lao PDR (Duckworth *et al*. 2010). Thus, this 1996 leaf monkey sighting could have referred to either Phayre's or a François'-group leaf monkey. That there are no further claims of Phayre's leaf monkey from this NPA, despite the many lengthy surveys there (cited in Duckworth *et al*. 2010), suggests that the animals were the latter.

In and around Phou Hinpoun (= Khammouan Limestone) NPA, Steinmetz (1998) received reports in January 1998 of a pale leaf monkey known as *taloung* from four villages, all in or close to massive karst, along the eastern edge of the NPA, two of which said it was extirpated, one of which said it was very rare, and the other reported it persisted; extensive interviews elsewhere in the NPA stimulated no reports of it (R. Steinmetz *in litt*. 2010). Yet further south (about 120 km south of confirmed records), Timmins and Khounboline (1996) considered that village reports in Hin Namno NPA (at Ban Vangngnow; 17°34'N, 105°48'E) of a long-tailed monkey, *taloung*, with white on lips and chin (indicated spontaneously, without reference to pictures), and living in forests on sandstone rather than the area's extensive karst (Duckworth *et al*. 2010: Table 4), probably referred to Phayre's; however, body color was said to be as François'-group leaf monkey (with which the informants were likely to be highly familiar, given its status in the general area). There remains no information from this area allowing solid identification, or even proof that any form of gray leaf monkey occurs there.

Thus, the true southerly extent of Phayre's leaf monkey in Lao PDR remains highly uncertain. The lack of records from intensive surveys in several areas south of its known records but north of known Indochinese silvered leaf monkey occurrence means that gray leaf monkeys can at best be only very rare in this region, at least nowadays. Timmins *et al.* (2011) pointed out that the parts of Lao PDR south of the northern highlands that lack confirmation of gray leaf monkey presence match well the distribution of red-shanked douc *Pygathrix nemaeus*. However, simple competitive exclusion may not be the whole explanation, because on the Nakai plateau, among the areas most intensively surveyed by direct observation for large mammals in the country (Dersu 2008), doucs are rare (Dersu 2008) and gray leaf monkeys unrecorded. This 1,250-km² area may have been suitable habitat for Phayre's leaf monkey as characterized above. It lies at 520–560 m, and (despite 25% of it being inundated for a reservoir in 2008) has a mosaic of semi-evergreen forest types including many rather open areas, and was crossed by a network of canopy-breaking streams and rivers. Tall bamboo was, however, localized and, overall, rare on the plateau although common on adjacent slopes. When surveyed most intensively, in 1994–1996, the plateau held populations of hunting-sensitive quarry species less depleted than those in most other surveyed parts of Lao PDR, with many records of macaques and gibbons (Evans *et al*. 2000; Dersu 2008), and it is highly implausible that Phayre's leaf monkey had previously occurred commonly but had already been hunted out.

Phayre's leaf monkey's known southern limit in Lao PDR (17°53'N; or even to 17°34'N, based on village reports) compares with occurrence in Vietnam south to southern Pu Mat Nature Reserve (*c*.18°46'N) as confirmed by recent records (Nadler *et al*. 2003); a skull lacking date of collection or identity of collector, labeled as from Tuyen Hoa district, Quang Binh province, suggests occurrence south to *c*.17°53'N (Fooden 1996; Nadler *et al*. 2003), matching well the Lao records. A claim of presence way further south, from the Kon Cha Rang – Kon Ka Kinh area (Gia Lai province; 14°09'–35'N, 108°16'–39'E) lacking any primary detail (Lippold 1995, 1998) is generally disregarded (Fooden 1996; Nadler *et al*. 2003). To the west of Lao PDR, in Thailand, there are solid records from much further south than in Lao PDR or Vietnam, to *c*.14°40'N in the west and to *c*.14°55'N in the east (Geissmann *et al*. 2004).

There is neither published nor, so far as we can trace, any specimen basis for Groves' (2001: p.268) statement that Phayre's leaf monkey extends to "southwestern Laos". However, there does seem conclusive evidence from two areas of Thailand (which lacks doucs) of very close approach and, in one, apparently, overlap of gray leaf monkey species (Geissmann *et al*. 2004: Fig. 3) so there may be surprises yet to be uncovered in Lao PDR in this group's distribution. Certainly, identifications as to the form of gray leaf monkey should not be made yet solely on the basis of locality.

Abundance

Only broad suggestions of abundance can be made pending specific study. These are based on contact rate in the various lengthy, direct-observation surveys in the species' Lao geographic range below 800 m altitude and on village opinion, on the assumption that all gray leaf monkeys within the species's Lao range are indeed Phayre's leaf monkeys. The several records from surveys with limited direct observation and/or focus on degraded areas, coupled with village information, suggest that the animal remains widespread in its Lao range. There tend to be only one or two records per survey area, and most villagers expressing opinion indicated scarcity of and/or large declines in this monkey (Hypa concession, HFI 1999; Nam Ha NPA, Johnson *et al*. 2003; Muang Vangviang, Duckworth in press; Phou Phadam, Phou Gnouey and Nongpet–Naxeng PFAs, Suford in press; and the lower Nam Ngiap, S. Watson *in litt.* 1999). No villagers seem to report stable or increasing populations, but many documents gave no information on this topic.

There is, therefore, no evidence of locally abundant populations of Phayre's leaf monkey presently in Lao PDR. Although there is insufficient historical information to be sure that it was ever markedly more common than it is now, the rate at which the Kelley–Roosevelts' expedition collected it in 1929 (Table 1) suggests that it may well have been. There is also no evidence of high-density populations in Vietnam, where hunting pressures on monkeys are very high (Nadler *et al*. 2003). It can, however, be very common elsewhere; for example, in the part of Phu Khieo Wildlife Sanctuary, Thailand, surveyed by Borries *et al*. (2002) it was by a fair lead the most common diurnal primate, and in North-east India, it is locally common although overall scarce (Choudhury 2001).

The questions most intriguing for conservation are perhaps "do the current generally low densities and apparent patchy distribution of Phayre's leaf monkey in Lao PDR reflect hunting, habitat/altitude factors, or both?", and thus, "were hunting relaxed, would populations expand significantly into habitats here considered unoccupied, or largely so?" The paucity of records of this monkey, and their opportunistic nature, prevents meaningful answers to these questions so far.

Conservation status

The number of Lao records in the 2000s, despite a decline in direct-observation survey since the 1990s (Duckworth 2008), indicates that the national conservation status of Phayre's leaf monkey is not as grim as feared by Duckworth *et al*. (1999). However, records are rather few, reflecting (and probably caused by) a general pattern of heavy hunting. Phayre's leaf monkey seems to survive in Lao PDR in most large tracts of forested land with significant areas below 800 m north/west of, and including, Nam Kading NPA. The large size of some such areas suggests that some large populations may persist. Given the differences in survey style, duration and personnel across the northern highlands in the

1990s–2000s, it is not possible to compare results from each site to pinpoint individual areas of special significance. Certainly, no relation should be taken between the number of records from an area and its likely importance to the species's survival prospects in Lao PDR.

The occurrence of this monkey in rugged landscapes, where hunting is less efficient and therefore less damaging than on the plains, probably is the major factor behind its healthier national conservation status than that of the congeneric Indochinese silvered leaf monkey. Nonetheless, under current hunting patterns, declines are likely to intensify and be followed by widespread extirpation. There are some large karst landscapes in the northern highlands which could offer better mid-term security even under current hunting (cf. Lao leaf monkey *T. laotum*; Steinmetz *et al*. 2011), but it is unclear whether Phayre's leaf monkey reaches comparable densities within them, or even occurs; they have been barely surveyed for mammals. Three of the NPAs with records (one only provisional) have active ongoing management-support projects: Nam Kading NPA (WCS 2010) and Nam Kan NPA (Robichaud *et al*. 2010) may support relatively large populations given their altitude and habitat, whereas Nam Et–Phou Louey NPA (WCS Lao Program internal documents) lies mostly over 800 m, and mostly well above this altitude.

Phayre's leaf monkey has an ambiguous legal status in Lao PDR. It is not explicitly mentioned by English or scientific name in the national Wildlife Law, but probably the listing given in Roman script as "silvered leaf monkey *Semnopithecus cristatus*", under the Lao name of "*khang* (*taloung*)" is best seen as for gray leaf monkeys of all species.

Even taking as the unit of analysis *T. p. crepusculus*, Phayre's leaf monkey numbers in Lao PDR are probably of rather little significance to global conservation compared with those in Thailand, which holds at least one high-density population over a large area (Borries *et al*. 2002). Lao populations of taxa like Lao leaf monkey and allies, red-shanked douc, and various *Nomascus* gibbons, are of far higher global significance, because the country holds most, in some cases the overwhelming majority of, surviving animals and retains much more extensive suitable habitat than does any other country (Timmins and Duckworth 1999; Duckworth 2008; Duckworth *et al*. 2010; Steinmetz *et al*. 2011). Additionally, Indochinese silvered leaf monkey is now very rare in Lao PDR, and its national extinction is probably looming without specific action to prevent it (Timmins *et al*. 2011). Phayre's leaf monkey is thus a lower priority than these species for specific action in the country. Fuller global contextualization of the significance of the Lao populations requires resolution of the uncertain taxonomy: in an east-of-Mekong context, Lao populations are probably much greater than those in Vietnam and China (see Zhang *et al*. 1992, Nadler *et al*. 2003).

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Distribution and Habitat of Assamese Macaque *Macaca assamensis* in Lao PDR, Including its Use of Low-altitude Karsts

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Abstract: The distribution and ecology of Assamese macaque *Macaca assamensis* remains little studied in South-east Asia. This review collates historical and recent records to clarify its range and habitat use in Lao PDR. Contrary to many standard sources limiting Assamese macaque's range to the north and center of the country, it occurs well into the southern part. In the country's three physiographic units, it is widespread in the northern highlands and the Annamite range, but seems absent from the Mekong plain. Most records are from hill evergreen forest above 500 m, consistent with standard literature, but the species occurs down to plains level (200 m) on karsts (at least in areas south of 16°58'N). The few records from below 500 m off karst are all in rugged terrain, but even so non-karst rugged land below 500 m seems to be only rarely used. Ecological overlap with northern pig-tailed macaque *M. leonina* and with Rhesus macaque *M. mulatta* is very limited in Lao PDR. In the long-term, hunting and forest encroachment may threaten Assamese macaque in Lao PDR, but it is much less imminently at risk in the country than are most gibbon and colobine species.

Key Words: Assamese macaque, *Macaca assamensis*, field identification, geographical distribution, habitat use, Laos, limestone

Introduction

Assamese macaque *Macaca assamensis* occurs from central Nepal east through the Himalaya to southernmost China and north and central South-east Asia (Fooden 1982). It has never had intensive field study anywhere in South-east Asia, or, barely, in South Asia (Mitra 2002, 2003), so remains little known for such a widespread monkey (Fooden 1982; Eudey 1991; Rowe 1996). It has conventionally been seen as a highland species: Lekagul and McNeely (1977), for example, called it "an upland macaque, generally found in forested areas above 500 m to as high as 3,500 m". Fooden's (1982) comprehensive review found most records from 150–1,900 m, with some up to 2,750 m (extended to 3,100 m by Fooden 1986), and a single, disjunct, record from sea-level (see below). A recent survey in Bhutan found Assamese macaques down to 600 m (Kawamoto *et al*. 2006); Choudhury (2008) referred to occurrences as low as 100 m but neither detailed nor discussed the record(s). Specifically in South-east Asia, records traced by Fooden (1982, 1986) were almost solely in mid- and high-elevation forest, with the lower hill records coming from South Asia.

Consistent with Fooden's (1982) conclusions, Ruggeri and Timmins (1997: 1) wrote that in the southern two-thirds of Lao PDR, "[Assamese macaque is] found predominantly in the evergreen forests of the Annamites [mountains]" but continued "it appears to be the most common species of macaque within areas of karst." Yet the relevant primary survey reports contain little information on this karst use in Lao PDR, this habitat use is omitted from some recent compilations (for example, Francis 2008), and the species was not even mentioned in a review of South-east Asian karst biota by Clements *et al*. (2006).

The present document therefore presents the records of Assamese macaques in Lao karst, in the context of as full a compilation as practicable of the species's records from all habitats in the country.

Survey areas and methods

Lao PDR is a landlocked country of 236,800 km², of three biogeographic divisions: the mountainous northern highlands and Annamite range, and the mostly lowland Mekong plain. Historical mammal collections in the country were few and, mostly, small (for example, Osgood 1932; Delacour 1940). During 1992–1998, many mammal surveys based on direct observation, mostly in support of the national protected area (NPA) system declared in 1993 (Berkmüller *et al.* 1995), clarified the status of numerous species across the country (Duckworth *et al.* 1999). The first four years of these surveys (late 1992 to mid-1996) generated over 300 sightings of diurnal primates (Ruggeri and Timmins 1997), although such survey activity has declined greatly since 1999. This review collates records of Assamese macaque from Lao PDR until early 2010. The many camera-trap photographs from Nakai–Nam Theun NPA in the 2000s, however, have not been reviewed, given the existence of many field records from this area in the 1990s.

Reviews of the Lao conservation status of red-shanked douc *Pygathrix pygmaeus*, diurnal squirrels (Sciuridae), François'-group leaf monkey *Trachypithecus francoisi* (*sensu lato*) and Lao leaf monkey *T.* (*f.*) *laotum* detailed the locations, methods and intensities of wildlife surveys in the 1990s–2000s (Timmins and Duckworth 1999, 2008; Duckworth *et al.* 2010a; Steinmetz *et al.* 2011). Of relevance to monkeys, most surveys were based upon direct daytime observation, unconstrained by any rigid search protocol, supplemented by searches for pets and remains of hunted animals in the field and in villages, and judicious use of local views on mammal status. For some surveys the text below expresses effort in terms of 'person-weeks'; the sum of all the field time of independently operating observers on the survey in question. A single observer for four weeks, a team of two making field observations together for four weeks, a team of two operating independently for two weeks, or a single person surveying half time for eight weeks (with, say, the other half spent in village-based activities) would all count as four person-weeks.

Five species of macaque inhabit Lao PDR (Duckworth *et al.* 1999) and their identification in the field requires care. During the 1990s, many encounters were left unidentified to species: the monkeys' habitual shyness meant that, if the animals were seen at all, it was often only poorly. Assamese macaque has a long history of range confusion through misidentification, discussed in detail by Fooden (1982). More recently and concerning Lao PDR, the photograph placed on the internet in support of the identification of Assamese macaque in the camera-trap survey of Nam Kading NPA reported by Ahumada *et al.* (2011) was of a northern pig-tailed macaque *M. leonina*, a species not identified by them at all. However, this misidentification was merely one of several elementary identification errors revealed by their placing their images on the internet; in reality, reliable identification of this species on camera-trap photographs is perfectly possible provided basic cares are taken.

In Lao PDR, the main confusion risk for Assamese macaque is Rhesus macaque: the two species have similar length tails, differing from those of the other three Lao macaques. Rhesus has rich rufous hindquarters contrasting with its non-rufescent forequarters, whereas Assamese has more uniform brown upperparts (often lacking any rufescence, but sometimes quite golden or even rufous) somewhat darkening to the forequarters, without contrasting russet on the haunches. It also has a call apparently not given by other Lao macaques: a high-pitched *eyou*, rapid and somewhat gull *Larus*-like (alternatively transcribed, in Myanmar, as *eeoow!*, recalling a deflating lorry air-brake). Diagnostic, but often not visible in the field, is the fore-crown hair arrangement, with a short 'parting' resulting from diverging hair tracts (versus a uniformly upwardly directed hair tract across the fore-crown of Rhesus). Assamese also seems always to lack two features sometimes shown by Rhesus, a darker cap and a red (often lurid red) perineal region; and, when present, its lengthy pale beard is diagnostic. Also, pale ischial callosities of Assamese macaques can be prominent at surprisingly long range. Tails can differ between the species, with that of the Rhesus macaque sometimes somewhat bicolored. The southern half of Lao PDR holds apparent intergrades between Rhesus and long-tailed macaques *M. mulatta* and *M. fascicularis*, which may have medium-length tails but reduced or absent rusty tones on the hindquarters (Fooden 1996, 1997). They are generally somewhat paler than more northern Rhesus macaques (Evans *et al.* 2000) and, as found by Eudey (1980) in part of Thailand, invite confusion with Assamese macaque.

Most identifications used several characters, and animals were generally observed as critically as their shyness allowed; some identifications had to remain provisional. Identifications from the early 1990s surveys were reviewed by RJT in the late 1990s and again during preparation of this manuscript, with increasing understanding of intraspecific variation in Assamese and Rhesus macaques in Lao PDR through extensive field experience (including in adjacent Vietnam), observations of many captive macaques of all Lao species, and review of literature. Two provisional Assamese macaque identifications were reassigned to Rhesus macaque, one corrected in Evans *et al.* (2000), the other being a 1996 observation from north of the Nam Theun below the Nam Theun 2 dam site (Dersu 2008). Several Assamese macaque records considered provisional at the time of survey were confirmed.

Village-derived information about macaques is not used here because the present authors, after experimentation, had no confidence that it could be used consistently for reliable species identification (see, for example, Duckworth *et al.* 2010a). Moreover, after far more extensive discussion with local people in several parts of Lao PDR, a surveyor much practiced in such techniques and fluent in Lao, Steinmetz (1998a: 7), wrote that "classification [to biological species] of the other local terms for macaques [additional to unmodified *ling*, which was linked for the survey area in question to pig-tailed macaque] is more obscure … For these reasons I will not attempt to sort out this confusion at this point… Field observation is required before definitive matches can be made". Similarly, after a nine-month village live-in, discussion-focused study in two Hmong villages of northern Thailand (adjacent to Lao PDR), Tungittiplakorn and Dearden (2002: 60) concluded that "an attempt to differentiate between species of monkeys was abandoned after many different and conflicting names and descriptions were received. One group

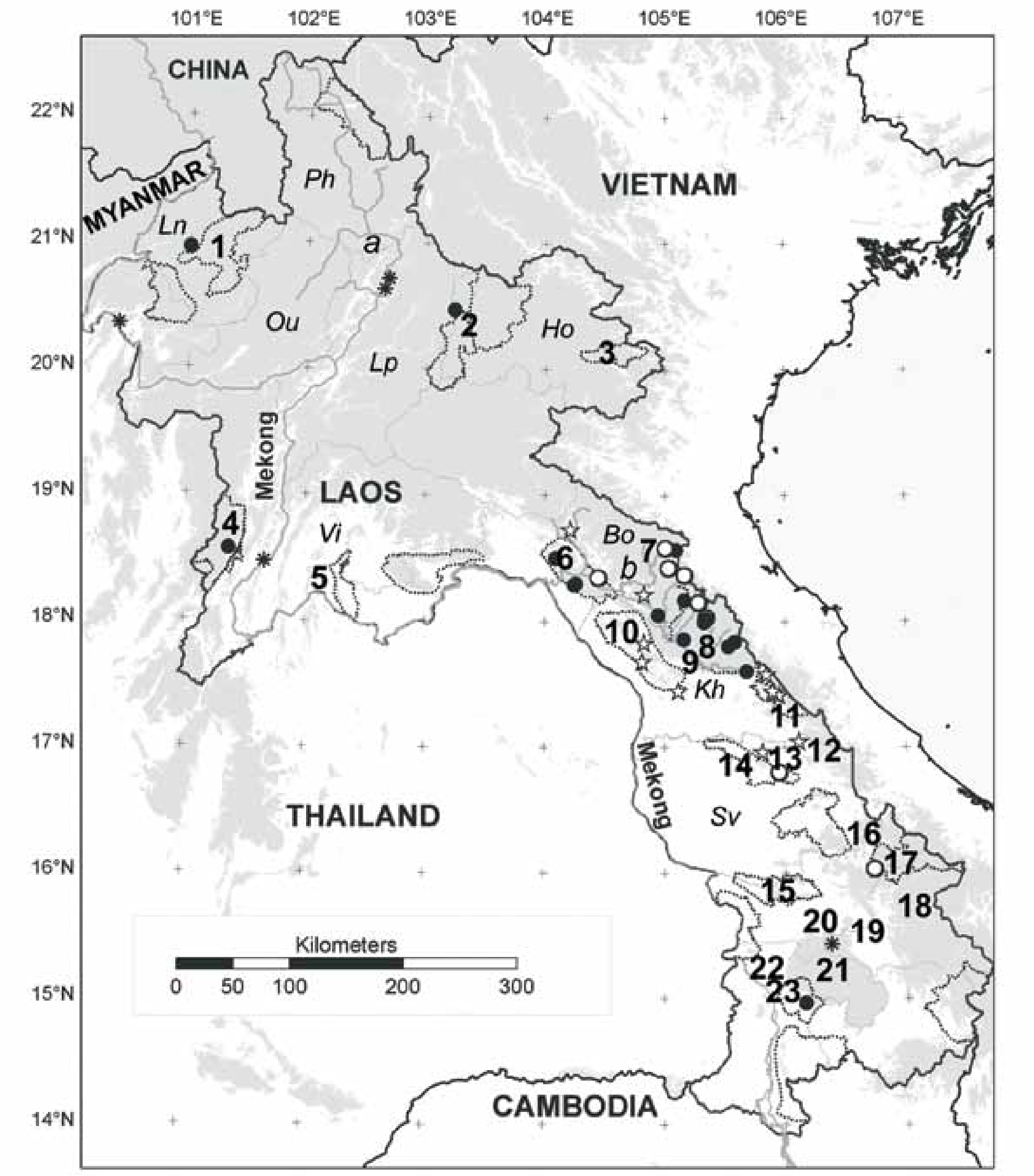

Figure 1. Lao PDR, showing localities mentioned in the text and records. Background shading shows land over 500 m. All national protected areas (NPAs) within the area covered, but only those provincial protected areas (PFAs), provinces, districts and rivers referred to in the text, are shown. The concentration of Assamese macaque records in central Lao PDR relative to the paucity further north at least mostly reflects distribution of survey effort, rather than relative abundance of Assamese macaques.

● modern record of Assamese macaque, away from karst, identification confirmed;

○ modern record of Assamese macaque, away from karst, identification provisional;

☆ modern record of Assamese macaque, on karst, identification confirmed;

* historical record of Assamese macaque.

Provinces: *Bo* = Bolikhamxai; *Ho* = Houaphan; *Kh* = Khammouan; *Ln* = Louangnamtha; *Lp* = Louangphabang; *Ou* = Oudomxai; *Ph* = Phongsali; *Sv* = Savannakhet; *Vi* = Vientiane.

Rivers: *a* = Nam Ou; b = Nam Kading (known as Nam Theun in it upper reaches).

Numbered areas: 1, Nam Ha NPA; 2, Nam Et–Phou Louey NPA; 3, Nam Xam NPA; 4, Nam Pouy NPA; 5, Muang Sangthong; 6, Nam Kading NPA; 7, Nam Theun Extension pNPA; 8, Nakai–Nam Theun NPA; 9, Nakai plateau; 10, Phou Hinpoun NPA; 11, Hin Namno NPA; 12, Laving-Laveun PPA; 13, central Muang Vilabouli; 14, Phou Xang He NPA; 15, Xe Bang-Nouan NPA; 16, Ban Somoy; 17, Xe Sap NPA; 18, Dakchung plateau; 19, Phou Theung plateau; 20, Ban Thateng; 21, Bolaven plateau; 22, Pakxe; 23, Dong Hua Sao NPA.

that was particularly difficult to identify was the macaques (genus *Macaca*).” These difficulties no doubt reflect the wide intraspecific age- and sex-related variation in appearance in macaques; and local perceptions of Assamese macaque as a unit distinct from other macaques is likely to be hindered by its lack of remarkable diagnostic visual characters. Thus, although interview-based surveys including macaques were conducted in parts of Lao PDR during the 2000s, their results are not considered here; none that we have seen documented any meaningful quality control assessment of reliability of macaque identifications to species, nor any triangulation of their results against field records.

Results and Discussion

General distribution in Lao PDR

Historical Assamese macaque records from Lao PDR were reviewed comprehensively by Fooden (1982). We have traced none other than the five specimens he listed (Appendix 1). Four were from the northern highlands, and the fifth from the Bolaven plateau in the south of the country. This southern specimen came from J. Delacour, who sometimes purchased animals in markets, but it seems unlikely to have been transported onto the plateau from anywhere else.

The 1990s–2000s surveys generated records from typical hill evergreen forest across much of the country (Appendix 2). These rather few records risk implying a misleading scarcity of the species in Lao PDR: that the field identification characters are subtle and need careful checking, yet animals are generally vigilant and shy, means that a lower proportion of actual Assamese macaque encounters will have been identified than with the other macaque species. And in the northern highlands it was simply very difficult to see and identify any macaques at all in the 1990s: in Nam Et–Phou Louey NPA macaques, always unidentifiable, were seen only four times during 14 person-weeks of field survey in 1998, and the only macaque firmly identifiable to species was a recently shot bear macaque *M. arctoides* (see Davidson 1998); the Assamese macaque group seen in Nam Ha NPA was the only macaque sighting firmly identifiable to species in 10 person-weeks, with only two sightings of unidentified macaques (Tizard *et al*. 1997); and there seem to have been no macaque sightings at all in six person-weeks at Nam Xam NPA in 1998 (Showler *et al*. 1998). A roadside survey of pet macaques in several northern highland provinces in May 2006 located 11, of which six were Assamese macaques (Hamada *et al*. 2007). Although the origin of these cannot be known, the high species proportion is consistent with the 1990s suggestions that this is the most numerous macaque of Lao hills and mountains. Hamada *et al*. (2007) found no more than two individuals of any other macaque species.

The Annamite range of Bolikhamxai and Khammouan provinces provided many records in the typical hill evergreen forest habitat. The Navang logging road (illicit; closed shortly after construction, and never used for timber extraction) into the heart of Nakai–Nam Theun NPA perhaps best indicated ‘natural’ status given the excellent long-distance viewing opportunities and (then) limited hunting of primates in the area: in 1996 the species was seen several times per week, spread across the upper 5 km of road surveyed (Duckworth 1998).

The Bolaven plateau in South Lao PDR, biologically a western outlier of the Annamites, holds Assamese macaque, but occurrence is not yet confirmed in the main Annamite range at these latitudes, with only one, provisional, field record. Additionally, two skulls from around the Dakchung plateau (*c*.15°30'N) of animals shot in 1993 are probably Assamese macaques (Bergmans 1995), and a captive that Steinmetz *et al*. (1999) saw in Ban Somoy (16°17'N, 106°54'E) is very likely to have been sourced locally (R. Steinmetz *in litt*. 2010). Kawamoto *et al*. (2006) recorded a pet Assamese macaque of unknown origin from Pakxe (15°07'N, 105°48'E), in the lowlands just west of the Bolaven plateau; but Pakxe is enough of a trading node that this should not be assumed to have been taken locally.

Despite extensive survey (see effort figures in Timmins and Duckworth 1999, 2008) in the several NPAs of the Lao Mekong plains, there are no records of this macaque from them, nor from the hills arising in their west, which are all rather low. And there is only one, evidently exceptional, from the well-surveyed Nakai plateau (Evans *et al*. 2000; Dersu 2008; U. Streicher *in litt*. 2010), a gentle plateau of 1,250 km² amid the Annamites (Dersu 2008) with Assamese macaque records in the hilly parts of the catchment both upstream and downstream of it.

The paucity of solid records (of any macaque species) from the northern highlands fits a general tendency for hunting-sensitive diurnal quarry species to be found much less often during direct survey there compared with areas in and south of the Nam Kading catchment (Fuchs *et al*. 2007; Duckworth 2008; Timmins and Duckworth 2008). This reflects differing

Figure 2. Pha Lom, north-east Savannakhet province, Lao PDR, 14 November 2008. Photograph by I. A. Woxvold. A small (*c*.800 m long × 250 m wide), isolated karst amid agriculture and degraded plains forest. In this landscape, Assamese macaques have been recorded only on the karsts.

patterns of hunting and, perhaps, use of forest for agriculture, which stem from the differing ethnic make-up across the country. The pattern is unlikely to reflect any inherent property of forests or climate, although historical collection effort was too meager to demonstrate that Assamese macaques were formerly more common in the northern highlands.

Karst records

Table 1 details records of Assamese macaque on Lao karst. The first record came during a short visit to Phou Hinpoun (= Khammouan Limestone) NPA, an area predominantly of massive karst, in 1994. Two subsequent short surveys of this NPA regularly found Assamese macaques on karst, and around this time there were also records from two nearby karsts, Pha Khok and Sayphou Loyang.

Hin Namno NPA is the only other NPA predominantly of karst. Here, single groups were found at all karst sites visited during a short survey in 1996, except for the only brief forays in the southern part of the NPA (Timmins and Khounboline 1996). A lengthier survey (7 person-weeks) during February–March 1998 (Walston and Vinton 1999) yielded six field sightings given as confirmed and three as provisional, a single freshly shot individual, and a village captive; some sightings were specifically noted as in limestone forest but it is not clear how many were. No information is given about altitude or precise localities. Moreover, J. L. Walston (*in litt*. 2010) cautioned that, reflecting the political complexities of this survey, some of the large mammal information incorporated may have been unreliable. This plausibly involved misidentification of Assamese macaques as other macaques, rather than vice versa, reflecting some team members' (whose survey time is excluded) belief that Assamese macaque is extremely rare.

Karsts were little surveyed from 1999 to 2007, but a 2008 visit to the southernmost canopy-breaking outcrops in Lao PDR, in western and central Muang (= district of) Vilabouli (north-east Savannakhet province), again found Assamese macaques on karst. Almost every protracted watch of a karst massif from neighboring plains (often rice fields) yielded a sighting, and the animals were indifferent to noise and movement of the people below. The animals were a good deal shyer when found by an observer himself within forest on Pha Kat's lower slopes. These Savannakhet records are of particular interest in several ways: some animals were almost

Table 1. Records of Assamese macaque *Macaca assamensis* from karst in Lao PDR.

Site name, location	Co-ordinates and altitude(s) of sighting	Date(s) of sighting	Reference(s)	Other notes
Phou Hinpoun NPA				
Near Ban Lak-9[1]	17°27'N, 105°07'E; *c*.300 m	23 May 1994	Evans *et al*. 2000	A group crossed a wooded karst cliff
Khuadin	17°50'N, 104°50'E; 220–300 m	7 & 8 Feb. 1996	Timmins 1997; RJT	Single groups in karst both days
Khuadin	17°50'N, 104°50'E; 250–270 m	17–19 Mar. 1998	Steinmetz 1998b, R. Steinmetz *in litt*. 2010	A group amongst huge boulders in karst forest
Kouan Houy	17°41'N, 104°49'E; *c*.200 m	1–5 Apr. 1998	Steinmetz 1998b, R. Steinmetz *in litt*. 2010	A group on sparsely vegetated sheer karst, rising above the semi-evergreen forest
Hin Namno NPA[2]				
Near the Houay Clocc	17°26'N, 105°55'E–17°25'N, 105°57'E; *c*.400–550 m	1, 3 & 4 Jan. 1996	Timmins & Khounboline 1996; RJT	
Near the Houay Pakha	17°27'N, 105°54'E; 250 m	5 Jan. 1996	Timmins & Khounboline 1996; RJT	
Houay Talee	17°35'N, 105°51'E; *c*.350–600 m	8 Jan. 1996	Timmins & Khounboline 1996; RJT	
Near the Houay Phasong	17°36'N, 105°50'E; 260 m	13 Feb. 1998	P. Davidson *in litt*. 2011	Two in rather deciduous forest near, but not on, karst
Near the Nam Ngo	17°30'N, 105°51'E; 200 m	15 & 16 Feb. 1998	P. Davidson *in litt*. 2011	A group in semi-evergreen forest at base of karst
Muang Vilabouli				
Pha Lom	16°58'N, 105°49'E; *c*.400 m	13 Nov. 2008; 15h15–15h30	JWD	A party of 13 (with one part-grown animal) moving across the higher, open, karst
Pha Lom	16°58'N, 105°49'E; *c*.400 m	3 Dec. 2008; 17h15	JWD	A troop of at least seven behaving as on 13 November
Pha Kat	17°03'N, 106°07'E; *c*.450 m	16 Nov. 2008; afternoon	JWD	Three sightings of single vigilant animals (?one individual) on the high west face
Pha Kat	17°03'N, 106°07'E; 260 m	20 Nov. 2008; 10h00	JWD	At least ten at a fruit tree in the evergreen forest growing from the karst base
Pha Kat	17°03'N, 106°07'E; 260 m	21 Nov. 2008; *c*.11h00	JWD	At least eight in a fruit tree in basal evergreen forest, then on karst face, *c*.1 km north of previous day's observation
Other areas				
Pha Khok, north of Nam Kading NPA	18°44'N, 104°13'E; 525 and 650 m	20 Mar. 1995	Evans *et al*. 2000; RJT	Perhaps two sightings of one group
Sayphou Loyang, near Ban Poung	18°14'N, 104°50'E; 725 m	13 May 1995	Evans *et al*. 2000; RJT	A group seen

[1] = Ban Lak Kao; date incorrectly given as 1995 in Evans *et al*. (2000).

[2] Does not detail most of the reported observations from a lengthier survey of Hin Namno NPA in 1998; see text.

at plains level; Pha Lom lacks any tall evergreen forest, supporting, where not bare rock, stunted open pachycaulous deciduous woodland (Fig. 2; shown in close-up in Woxvold *et al.* 2009: Plate 4); and these karsts, unlike those in Phou Hinpoun and Hin Namno NPAs, are small outcrops isolated amid non-karst habitat: even Pha Kat, the biggest, is only *c*.2.5 km². No other macaque was observed on these karsts, although pig-tailed, Rhesus and bear macaques were all found in the survey area (Duckworth *et al.* in prep.).

These records of karst-living Assamese macaques come from three contiguous provinces in central Lao PDR (Savannakhet, Khammouan and Bolikhamxai). Karsts are also extensive in the country's northern highlands, but—here lying largely outside the national protected area system—have been barely surveyed for mammals, and their macaque species are unknown.

In sum, karst use is typical of Assamese macaque in Lao PDR, and this macaque is a feature of Lao karst landscapes, at least in the central provinces.

Overall habitat use

Ruggeri and Timmins (1997: 1) stated that Assamese macaque was "rarely encountered in heavily degraded or semi-deciduous habitats" in Lao PDR, and subsequent records away from karst gave nothing to modify this conclusion. Nearly all Lao records traced were from evergreen forest, consistent with Fooden's (1982) profiling of it as a species that is almost completely arboreal and strongly associated with dense evergreen forest. He found that records from deciduous areas, bamboo and cultivation were all from close to this main habitat. Lao records outside evergreen forest comprised several from karst supporting largely deciduous vegetation (both Pha Lom and Pha Kat, Savannakhet province), and from the foot of the Bolaven plateau slopes in Dong Hua Sao NPA where the animals were in semi-evergreen forest with a high proportion of deciduous trees.

Away from karst, most records came from above 500 m, with the lowest from somewhere between 200 and 400 m (imprecisely recorded; and only provisionally identified), and the next lowest from 400 m. By contrast, karst records came down to 200 m, with occurrence at six sites in the 200–400 m band. The use of karst at altitudes lower than typical in non-karst habitats may reflect its steep topography. Assamese macaques seem effectively absent from non-rugged terrain below about 500 m, as shown by the several surveys in the Lao range of Assamese macaque (i.e., Bolaven plateau and northwards) which did not find it despite a fair number of records of other monkeys and of gibbons: Nakai plateau (Dersu 2008 and references therein; one subsequent record of Assamese macaque); Xe Bang-Nouan NPA (Evans *et al.* 2000); Muang Sangthong, Vientiane municipality (Duckworth 1996); Phou Xang He NPA outside Phou Hinho (Duckworth *et al.* 1994); non-karst parts of western and central Muang Vilabouli, Savannakhet province (Duckworth *et al.* in prep.); and the Phou Theung plateau (Timmins 2009). There are also substantial areas below 500 m in Lao PDR on rugged terrain that are not karst. These have not been as well surveyed as karsts at comparable altitude, but in sum the paucity of records from such altitudes in Nam Kading NPA (Evans *et al.* 2000, Timmins and Robichaud 2005), two production forest areas in Vientiane province (Suford in press), Laving-Laveun Provincial Protected Area (Duckworth *et al.* 2010b), and the Phou Hinho part of Phou Xang He NPA (Duckworth *et al.* 1994), suggests a general scarcity in such habitat. The cited surveys of all these sites detected other species of monkey and gibbons fairly often.

Karts's expanses of bare rock (bigger and more numerous than in most non-karst habitats) may themselves be important to Assamese macaque. In Nepal, sleeping sites in hill evergreen forest are typically rocky cliffs, usually devoid of trees and shrubs, and presumably selected to minimize risk of attack by predators (Chalise 2003); in West Bengal the species was said to prefer rocky terrain and hill slopes (Mitra 2002); and seven of eight sightings in Mizoram, India, by Raman *et al.* (1995: 60) were "along cliffs with primary vegetation," the other being "close to the cliff face." Although in Bhutan "rocky cliffs with sparse vegetation" are an apparently minor habitat (Choudhury 2008: 66), field contacts with the species in western Thailand were in forest by or on rocky mountains (Eudey 1991).

At lower altitudes, Assamese macaques may require steep cliffs; but they do not at higher altitudes: in parts of interior Nakai–Nam Theun NPA, the species occurs far from cliffs. Cliffs might serve as sleeping sites. Although Fooden (1986) traced no information on such sites and speculated that the species would be found to sleep in trees, Eudey (1991) thought that in Huay Kha Khaeng Wildlife Sanctuary it slept in protruding crags or the large trees adjacent to them, and the subsequent information (above) from other countries indicates use of cliffs as sleeping sites. There remains no information on where Assamese macaques sleep in Lao PDR; Walston and Vinton (1999: 23) wrote of "two groups seen at sleeping sites at Khoaymep forest," but no details are now available, including confirmation of identification (J. L. Walston *in litt*. 2010). In Lao PDR, the karst itself is used for travel (even over hundreds of meters) and to provide look-out perches when most of a troop is feeding in karst forest, from which most records in karst landscapes came.

Karst and low-altitude records from other countries

There are various records from karst landscapes in Vietnam (Nisbett and Ciochon 1993), notably Phong Nha–Ke Bang National Park (Timmins *et al.* 1999; Haus *et al.* 2009), and also the Nui Giang Man area, Di Gia Nature Reserve and Na Hang Nature Reserve (Nadler *et al.* 2004). These documents do not detail altitudes of observation and are rarely explicit whether macaques were on the karst: therefore it is not possible to tell whether there is the same habitual karst use, and a similar difference in altitudinal occupation between karst and non-karst areas, in Vietnam as in Lao PDR. In Myanmar, Anderson (1879) noted a large group of Assamese macaques on the bank of the Irrawaddy downstream of Bhamo (24°16'N, 97°14'E), below a huge limestone cliff. The Irrawaddy here is at *c*.100 m, indicating lowland karst use also in that country. These animals were artificially provisioned, so it is unclear whether this was their natural habitat. In Thailand, detailed information comes from three karsts around Buddhist temples, where Assamese macaques occur down to 400 m (Aggimarangsee 1992); as in Lao karst, this is perhaps rather low for the species in South-east Asia. Off karst in Thailand, Assamese macaque was encountered regularly in dry evergreen forest in Phu Khieo Wildlife Sanctuary during a study at 600–800 m (Borries *et al*. 2002), and in an altitudinally wide-ranging study in Huai Kha Khaeng Wildlife Sanctuary it was found between 700 and 1,400 m (Eudey 1991); but little else specific seems to be available on altitudinal distribution in the country.

A superficial check of information from elsewhere in the species' range showed no discussion of karst use, although occasional reference is made to occurrence in areas containing some karst (for example, Yimkao and Srikosamatara 2006). Several other records indicate lowland occupancy, for example, on the floodplain of Dibru–Saikhowa National Park, Assam, India (Choudhury 2001). There is one essentially sea-level record: from the Sundarbans coastal swamps of Bangladesh, *c*.50 miles east of Calcutta (Anderson 1872). Fooden's (1982) careful review found no reason to doubt this record. In fact, Anderson's (1872) account has several strong points: having heard rumors of two sorts of macaques from local inhabitants of the Sundarbans, the descriptions of which fitted Rhesus and Assamese macaques, he sent his collector to the area, who returned with undoubted examples (identifications re-validated a century later by Fooden's own examination) of both species. This contemporary awareness means a curatorial error in the interim (for example, erroneously inferred locality, or mis-association of specimen and tag) can be discounted. Nonetheless this record is extraordinary, causing doubts in some present-day quarters. Nearby there are neither modern records of Assamese macaque (despite fairly heavy wildlife survey and research presence), nor any hills, even small ones, let alone karst. The nearest hill-forest where Assamese macaque would be expected (and indeed occurs) lies approximately five times the distance further east of Calcutta, so a mistake over locality seems unlikely (Md. Anwarul Islam *in litt*. 2010, P. M. Thompson *in litt*. 2010). The only possibility for error seems to be a dishonest collector who for some reason falsified the locality.

Ecological overlap with Rhesus macaque

Fooden (1982) concluded that Assamese macaque was ecologically parapatric with, respectively, pig-tailed and Rhesus macaques. Recent Assamese macaque records in Lao PDR overlapped geographically and altitudinally with both these species, but ecological separation may well nonetheless be strong. This review traced no Lao records of Rhesus macaque in karst; it occurs predominantly in stream-side and degraded areas. In these latter habitats Assamese macaque has not been recorded in Lao PDR, but there is some overlap in adjacent countries. In the Hukaung valley of northern Myanmar, along the Tarung Hka (a river), on 21 January 2006 a troop of about 20 Assamese macaques was seen on low bedrock exposed from the river's banks, with several down at the water's edge, at *c*.26°47'N, 96°31'E; and that evening a group of a score or so was seen apparently settled for the night in a streamside giant tree, at *c*.26°45'N, 96°29'E. Yet Rhesus macaques were commonly observed along this river, and others, in the Hukaung valley (JWD). In Vietnam, Nisbett and Ciochon (1993: 788) surmised that Rhesus macaque "lives in virtually all forest types except karst forest." Hill (1999), however, noted several records apparently from limestone forest of Ba Be National Park and perhaps other sites, but the basis for identification of these was not discussed.

Ecological overlap with northern pig-tailed macaque

Northern pig-tailed macaque has recently been found much further north in Lao PDR than suggested by records available to Fooden (1982). It occupies the Mekong plain north to at least Muang Sangthong, Vientiane municipality (Duckworth 1996) and even the lower hills in two northern areas supporting Assamese macaques, Nam Kading and Nam Pouy NPAs (Boonratana 1997; Evans *et al*. 2000). Persistent reports, but based only upon village information, suggest that pig-tailed macaque may occur north even to Louangnamtha province (Tizard *et al*. 1997; Johnson *et al*. 2003; Hamada *et al*. 2007) and while observations of two captives (in Oudomxai and Louangnamtha provinces; Hamada *et al*. 2007) provide some support for this, there is yet no direct field verification. Suitable, albeit generally rather small, lowland areas for pig-tailed macaque occur even into the northernmost province, Phongsali (for example, around Ban Muangyo; Fuchs *et al*. 2007). Such areas have been poorly surveyed for mammals. They are heavily settled and hunting levels are very high, so the pre-exploitation relative distribution of Assamese and pig-tailed macaques in northern Lao may never be determined.

There are too few records with precise altitudes to assert the degree of altitudinal overlap between these two species in hill evergreen forest: available Lao observations fit Fooden's hypothesis that Assamese generally lives higher than pig-tailed, although the two have been seen in several areas in similar habitat and altitude: on the Nakai plateau (only one Assamese macaque record, many pig-tailed; Evans *et al*. 2000; Dersu 2008; Appendix 2) and in Phou Xang He NPA (where both species were seen on the same day and in the same valley in the Phou Hinho sector (RJT); and, to some extent, in Nam Kading NPA (where a group of pig-tailed was recorded in the lower Nam An valley at 300 m, well below the records of Assamese) and at the foot of the Bolaven slope in Dong Hua Sao NPA (with the pig-tailed macaque record on the adjoining plains; RJT). In and around the main karst areas, however, there is coarse overlap but Assamese macaque has not been recorded far off karst whilst pig-tailed has been found only very rarely on it. There were two pig-tailed macaque records explicitly from karst in Hin Namno NPA in 1998 (Walston and Vinton 1999; but see caution above); at Kouan Houy, Phou

Hinpoun NPA, during 1–5 April 1998, a troop of about 17 pig-tailed macaques was seen on sparsely vegetated karst cliffs, where Assamese macaques were also recorded, but in different portions of the cliffs (Steinmetz 1998b); and in extensive karst north of Phou Hinpoun NPA, 2 km from Ban Nahin at the plain's edge (*c.*18°11'N, 104°29'E), J. Eaton (*in litt.* 2011) saw a lone male pig-tailed macaque on 28 December 2009, and a female with young (at 150 m a.s.l.) on 26 January 2011.

Southern range margin in Lao PDR

The southernmost Lao record of Assamese macaque, in Dong Hua Sao NPA at 14°58'N, is similar to the southernmost published record globally, from Chongkrong, Thailand (of 14°41'N, 98°52'E), close to the Myanmar border (Fooden 1971; Groves 2001). Francis's (2008) generalized range map indicates presence slightly further south in Vietnam. This map stems from a discussion for the 'South-east Asian Mammal Databank' and no original data are available (C. M. Francis *in litt*. 2010); its boundaries may be predictive, not evidentiary. Fairly detailed and extensive primate surveys some way north of this boundary, in Quang Nam province, at latitudes similar to the Bolaven plateau, did not find Assamese macaque at all (Minh *et al*. 2005), and Nadler *et al*. (2007: 11), stating that "the distribution in Vietnam is not very clear yet", knew of no records south of Phong Nha–Ke Bang NP (*c*.17°30'N). Although Fooden (1982) had detailed the 1931 Bolaven record, various key sources persist in confining the Lao distribution to the north of the country (for example, Corbet and Hill 1992; Rowe 1996; Brandon-Jones *et al*. 2004; Nadler *et al*. 2007).

National conservation status

The Assamese macaque ranges widely in Lao PDR, inhabits many protected areas, some of over 2,000 km² and some with extensive rugged terrain in which hunting is difficult, and persists even on small isolated karsts. Thus, it is unlikely to be imminently threatened in Lao PDR (see discussion in Timmins and Duckworth 1999; Steinmetz *et al*. 2011; Timmins *et al*. in press a, in press b). The paucity of records from the northern highlands could suggest widespread major declines. However, survey effort there was too low to detect many macaques by direct sighting (see above): recent camera-trapping in this area, in Nam Et–Phou Louey NPA, found bear macaque to be among the most commonly photographed mammals (Johnson *et al*. 2006). This NPA had more direct-observation survey effort in the 1990s than any other northern highland NPA, yet there were no field sightings of bear macaque. Unlike bear macaque, Assamese macaque is not sufficiently ground-dwelling to be readily camera-trapped, forestalling independent triangulation of its abundance in the northern highlands. But, because much hunting in the northern highlands is by snaring, the more arboreal Assamese macaque should be less depleted than is bear macaque.

There is therefore no reason to expect major declines of Assamese macaques within the NPAs and other large, remote blocks of habitat in the short- to mid-term; but, as with all quarry species, the barely-restrained hunting of almost all mammals of domestic cat-size and larger, coupled with piecemeal and sometimes major (for example, new road) encroachment into remote forests, pose a severe long-term threat in the country. In sum, in a world of finite resources for conservation, Assamese macaque is of much lower in-country conservation priority than are the gibbons and most colobines (Timmins and Duckworth 1999; Duckworth 2008; Duckworth *et al*. 2010a; Coudrat *et al*. in press; Timmins *et al*. in press a, in press b).

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Appendix 1. Historical records of Assamese macaque *Macaca assamensis* from Lao PDR[1].

Site name, location	Altitude(s) of collection	Date(s) of collection
Beside Ban Muangngoy, 20°43'N, 102°41'E	Unknown[2]	28 Nov. 1931
Along the Nam Ou 80 km upstream of Ban Pak-Ou, 20°38'N, 102°39'E	Unknown	21 Jun. 1924
Lo-Tiao, 20°20'N, 100°25'E	*c*.1,500 m	5 Jan. 1939
Near the Mekong 110 km west-north-west of Vientiane, 18°28'N, 101°40'E	Unknown	4 Jul. 1924
Ban Thateng[3], Bolaven plateau, 15°26'N, 106°23'E	village: *c*.900 m	14 Dec. 1931

[1] Deuve (1972), in a purportedly comprehensive review of the mammals of Lao PDR, did not include the species; given his many other basic errors (see, for example, Timmins and Duckworth 1999) this should not be seen as indicating even scarcity in, still less absence from, Lao PDR at that time.

[2] "Half-way up the mountain" (Legendre 1936: 158).

[3] Duckworth *et al*. (1999) spoke of multiple specimens from Thateng, but this seems to have been a slip; Fooden (1982) listed only one, and we know of no others.

Appendix 2. Recent (1992–early 2010) field records of Assamese macaque *Macaca assamensis* in non-karst habitats of Lao PDR.

Site name, location	**Co-ordinates and altitude(s) of sighting**	**Date(s) of sighting**	**Reference(s)**	**Other notes**
Northern highlands				
Nam Et–Phou Louey NPA	20°28'N, 103°14'E; 1,250 m	10 Apr. 2005; 15h08	A. Johnson *in litt*. 2011	Camera-trap record[1]
c.2 km north of Ban Tonglat-kao, Nam Ha NPA	20°58'N, 101°00'E; within 1,200–1,400 m	Feb. 1997	Tizard *et al*. 1997; P. Davidson *in litt*. 2010	
Central Nam Pouy NPA	18°34'N, 101°22'E; *c*.500 m	4 May 1997	Boonratana 1997; RB	Group of *c*.20
Annamites				
Nam Kading NPA	18°30"02"N, 104°05'37"E; 750 m	24 Dec. 2007 (14h57 & 15h04)	A. McWilliam *in litt*. 2010	Camera-trap record
Upper Nam An valley, Nam Kading NPA	18°18'N, 104°16'E; 745 m	14 Apr. 1995	Evans *et al*. 2000	
Upper ridge of the Nam An catchment, Nam Kading NPA	18°17'21"N, 104°14'51"E; 900 m	22 Apr. 1995	Evans *et al*. 2000; RJT	
North slope of Sayphou Ao, Nam Kading NPA	18°21'N, 104°27'E; *c*.550 m	2 May 1995	Evans *et al*. 2000; RJT	Provisional
Ridge south of the Nam Theun below the Nam Theun 2 dam-site	18°03'N, 104°57'E; 730 m	18 Feb. 1996	Dersu 2008; RJT	
North of Ban Nakadok, Nakai–Nam Theun NPA	18°11'N, 105°10'E; 750 & 850 m	[14] and 15 Jan. 1994	Evans *et al*. 2000	Two records, one provisional
Middle Nam Xot valley, Nakai–Nam Theun NPA	18°08'N, 105°15'E; *c*.725 m	18 Jan. 1994	Evans *et al*. 2000	Provisional
Navang logging road, Nakai–Nam Theun NPA	*c*.18°01'N, 105°21'E; *c*.1,200 m	21 Apr. 1994	Evans *et al*. 2000	Provisional
Navang logging road, Nakai–Nam Theun NPA	17°58–18°02'N, 105°19–21E; across 1,000–1,300 m	24 Apr. – 14 May 1996	Duckworth 1998	Many records
Navang logging road, as above	Across 1,100–1,200 m	within 24 Feb. – 5 Mar. 1997	WCS 1997	Three records
Houay Morrow, Nakai–Nam Theun NPA	18°01'N, 105°21'E; 800 & 900 m	26–27 Feb. 1997	WCS 1997	Two records
Upper Nam On valley, Nakai–Nam Theun NPA	17°36'N, 105°41'E; *c*.780–880 m	Dec. 1995	W. G. Robichaud *in litt*. 1996	
Near Ban Kunaeh, Houay Manthon, Nakai–Nam Theun NPA	17°50'N, 105°35'E; *c*.820 m	26 Nov. 1998	Robichaud & Stuart 1999; W. G. Robichaud *in litt*. 2010	
Between Thong Khouang and Ban Nameo, Nakai–Nam Theun NPA	17°48'N, 105°32'E; 750 m	12 Dec. 1998	Robichaud & Stuart 1999; W. G. Robichaud *in litt*. 2010	
Nam Phao, Nakai–Nam Theun NPA	18°22'N, 105°10'E; 900 m	within 20–22 Mar. 1997	WCS 1997	Provisional
Phou Chomvoy, Nam Theun Extension pNPA	18°25'N, 105°03'E; 1,000 m	within 28 Mar. – 3 Apr. 1997	WCS 1997	Provisional
Tributary of the upper Nam Tang, Nam Theun Extension pNPA	18°34'N, 105°06'E; *c*.750 m	8 Jun. 1998	Robichaud & Stuart 1999; W. G. Robichaud *in litt*. 2010	
Tributary of the Nam Ta, Nam Theun Extension pNPA	18°34'N, 105°00'E; 550 m	31 May 1998	Robichaud & Stuart 1999; W. G. Robichaud *in litt*. 2010	Provisional
Nakai plateau	17°50'37"N, 105°11'26"E; 560 m	6 Feb. 2010	RJT	In mixed pine and semi-evergreen forest on gentle terrain
Phou Hinho, Phou Xang He NPA	16°48'N, 105°57'E within 200–400 m	15 Apr. 1993	Duckworth *et al*. 1994, RJT	Provisional
Western slope of Phou Leng, Xe Sap NPA	16°02'N, 106°44'E; 800 m	within 15–20 Mar. 1999	Steinmetz *et al*. 1999	Provisional
Bolaven slope near Ban Houayton, Dong Hua Sao NPA	14°58'N, 106°10'E; *c*.400 m	11 Jul. 1993	Duckworth *et al*. 1994, RJT	

All records are direct sightings except where stated.
NPA = National Protected Area; pNPA = proposed National Protected Area.

[1] Johnson *et al*. (2006) referred to Assamese macaque being camera-trapped in this NPA in 2003–2004, but re-examination of the photographs by RJT, JWD and A. Johnson found that the record in fact probably is of Rhesus macaque *M. mulatta* (as had been earlier indicated in Johnson *et al*. 2004).

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A New Color Morph of the Southern Purple-faced Langur (*Semnopithecus vetulus vetulus*) from the Rainforests of Southwestern Sri Lanka

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Abstract: The southern purple-faced langur (*Semnopithecus vetulus vetulus*) is endemic to Sri Lanka and is listed as Endangered on the IUCN Red List. Following several decades of widespread deforestation in the country, viable habitat has been severely reduced for these arboreal, folivorous primates. Living close to densely populated human settlements has lead to further conservation difficulties. They have adapted to exploiting cultivated fruits in home gardens resulting in human-primate conflict, besides confronting electrocution hazards when crossing roads using power lines. The opening of the Colombo-Matara Expressway has also posed a threat, with the possibility of troops from either side becoming genetically isolated. Twenty-six troops were studied from 2007 to 2011 in the southwestern districts of Galle and Matara; of these, 14 contained one or more individuals with an atypical pelage coloration, which we call here a white color morph. Two white alpha males were documented, along with adults, juveniles, and young of both sexes, totaling 30 individuals. The troops around Deniyaya and Getabaruwa villages contained members that showed a distinct pelage, and all of the members of these troops had dissimilar cranial features and body size compared to other *S. v. vetulus*. Molecular analysis is now required to discover the genetic basis for this variation and any possible competitive advantages associated with its spread, with the possibility that this may originate a new subspecies. The discovery of a new color morph may provide an additional opportunity to promote primate conservation; greater national support is urgently needed considering the perilous future facing *S. vetulus*. Further research prospects and conservation recommendations are discussed in this paper.

Key words: Purple-faced langur, *Semnopithecus vetulus*, Sri Lanka, endemic species, endangered species, color morph, conservation

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Introduction

The purple-faced langur, *Semnopithecus vetulus* (Erxleben, 1777), was previously classified in the genus *Trachypithecus* Reichenbach, 1862. *Trachypithecus*, however, is currently considered to encompass solely the Southeast Asian langurs (Molur 2003; Brandon-Jones 2004; Dela 2007). Recent molecular analysis of several colobine species by Karanth *et al.* (2008) has determined the Nilgiri and Sri Lankan langurs to phylogenetically cluster with the Hanuman langur (*Semnopithecus*) at three sequenced markers, whereas the langurs of Southeast Asia (*Trachypithecus*) form a distinct clade (see also Osterholz 2008). Despite this evidence, several studies classify the species in the genus *Trachypithecus* (Groves 2001, 2005; Rudran 2007; Parker 2008). This paper should provide ample opportunity for further genetic research into the species, aside from the current classification debate.

The purple-faced langur is endemic to the island of Sri Lanka and is represented by four allopatric subspecies, each from different geographical zones (taxonomy following Groves 2001). The focal subspecies of this paper — the southern purple-faced langur, *Semnopithecus vetulus vetulus* — is found in the Wet Zone and classified as Endangered on the IUCN Red List (2011). Agricultural development and irrigation, along with spreading human settlements, have been destroying the Sri Lankan rainforest for decades (Erdelen 1988). Today, much of the rainforest is fragmented, and troops that inhabit home ranges bordering suburban areas inevitably exploit agricultural land for food. Conflict in southern areas may alter perceptions of the purple-faced langur, currently considered to be a pest in the more populated

Western province, where it is the most common primate (Dela 2007; Rudran 2007). However, people sharing their gardens are generally tolerant owing to religious and cultural beliefs, which prohibit harming animals, leaving habitat loss as the most important threat (Nahallage 2008).

Sri Lanka's industrial growth requires a corresponding infrastructure; the first phase of the Colombo-Matara Expressway, linking the capital city to as far south as Galle, was scheduled to open September 2011. All of the troops in this study are to the northeast of the expressway, and the troops 15–20 km from the coast in both the Southern and Western provinces will now have little to no contact with the main island population. The occurrence of fatal electrocutions is linked to their strong preference to remain above ground during even minor road crossings, to avoid both vehicles and dogs (Moore 2010). It is predicted that the expressway will completely isolate numerous troops from the genetic pool of the rest of the island.

The majority of *S. vetulus* research is focused on the Critically Endangered western purple-faced langur (IUCN 2011), *S. v. nestor* Bennett, 1833. Therefore, it was decided by the team at the Wildlife Conservation Society Galle to undertake research on the southern subspecies, in the face of escalating conservation issues. Investigations of this scale had not been attempted in Sri Lanka previously; the specific aim was to assess group composition and behavioral changes when the langur is in an anthropogenic landscape. The unexpected discovery of a striking new color morph shows the limitations of our knowledge, and how much more scope remains for research and conservation of purple-faced langurs.

Methods

The study was conducted in the southwestern districts of Galle and Matara, in the wet zone of Sri Lanka. Data on langur group composition were collected between May 2007 and January 2011 by members of the Wildlife Conservation Society Galle (WCSG), based at Hiyare Rainforest Reserve. Troops were approached on foot, and habitat was categorized as tea plantation, home garden, or rainforest. Recordings of the latitude and longitude were taken using a Garmin Etrex Vista H when the troop was first encountered. Exact location was recorded only once as the home range of the purple-faced langur is exceptionally small, averaging 2–3 ha (Rudran 1973a). Troops were allocated a troop identification number, and individual group members were numbered; for example, T18-I5 was a white alpha male in group T18 situated near Wathugala (Fig. 1a). The initial sighting of a troop was followed by an intensive period of study (from 15 to 25 days), until each individual was identified. Identification cards for each individual combined the unique identification number with an annotated sketch with identifiable markings.

In the typical dark color morph individuals, the pelage characters allowed sex determination of the adults (Rudran 1973a). Sub-adult and infant females do not have the identifiable white pubic patch, and sexing of younger individuals was only possible if the gonads were visible. The white color morph adults were also sexed using this method, or occasionally sex could be determined when they were seen mating. Age (adult, sub-adult, infant) was estimated based on body size (Rudran 1973a).

The initial study phase allowed the troops to habituate to the researchers and photographers, allowing visual contact to be maintained almost entirely throughout the study. During the initial research period, troops were studied from 06:00 to 10:00 and 16:30 to 18:30 each day. Talking with the local people allowed us to locate the troops quickly whenever we returned for further observation. Behavioral recordings were made only after habituation using Nikon Monarch 8 × 32 binoculars. Photographs were taken using a Canon 7D body with Canon 500 mm F4 lens.

Results

External morphological traits of the new color morph

The southern subspecies is primarily distinguishable by a defined silver-white rump patch; a detailed description of the standard pelage characters has been documented by Phillips (1935; Fig. 1b). The newly discovered color morph has a white body and limbs, sometimes with ashy patches, and a white tail (Fig. 1a, Fig. 2). The underparts have pink and yellow skin tones visible through white hair, and the hands and feet are similarly pink-and-yellow toned with black patches. The head has white or off-white whiskers, the throat patch and hairs around the mouth are also white and the crown is of beige to ashy brown hair. Naked parts of the face and ears are black and the eyes have a golden brown iris, as with the standard color morph.

There is no evidence to suggest albinism for the following reasons: all white individuals have a black face, none of the white individuals have red eyes, and all of the white individuals have an ashy brown crown of hair. Among the Colombo National Museum primate collection a pale-colored specimen was collected by Phillips from the Matara District as early as 1923 (catalog number 4G 20.11.1923), evidencing that a slight degree of color diversity among the Southern purple-faced langur is not uncharacteristic (Fig. 3).

External morphological traits of the Deniyaya and Getabaruwa troops

Distinct morphological features are shown by both standard and white color morph members of troops in the vicinity of Deniyaya and the southwestern village of Getabaruwa (Deniyaya: 6°20'42"N, 80°33'37"E, Getabaruwa: 6°19'09"N, 80°33'04"E), which are 7.25 km apart. The body size of all troop members is smaller in comparison to normal *S. v. vetulus*. Cranial differences in all troop members include a more flattened brow profile, longer and more curved whiskers, and a darker brown crown of hair (Fig. 4). The standard color morph is darker and the pubic patch appears brighter and more prominent.

Figure 1. A comparison of the newly discovered color morph to the standard pelage; a) a white colored alpha male from troop 18; b) a troop 14 member with the standard color morph of *S. v. vetulus*. Photographs by Nadika Hapuarachchi.

Figure 2. An individual showing ashy patches on the body and limbs during locomotion. Photograph by Nadika Hapuarachchi.

Figure 3. Museum specimens collected by Phillips from the Matara district in 1923. A degree of color diversity can be seen between the lower standard color specimen (4F, 02/12/1923) and the lighter individual above (4G, 20/11/1923).

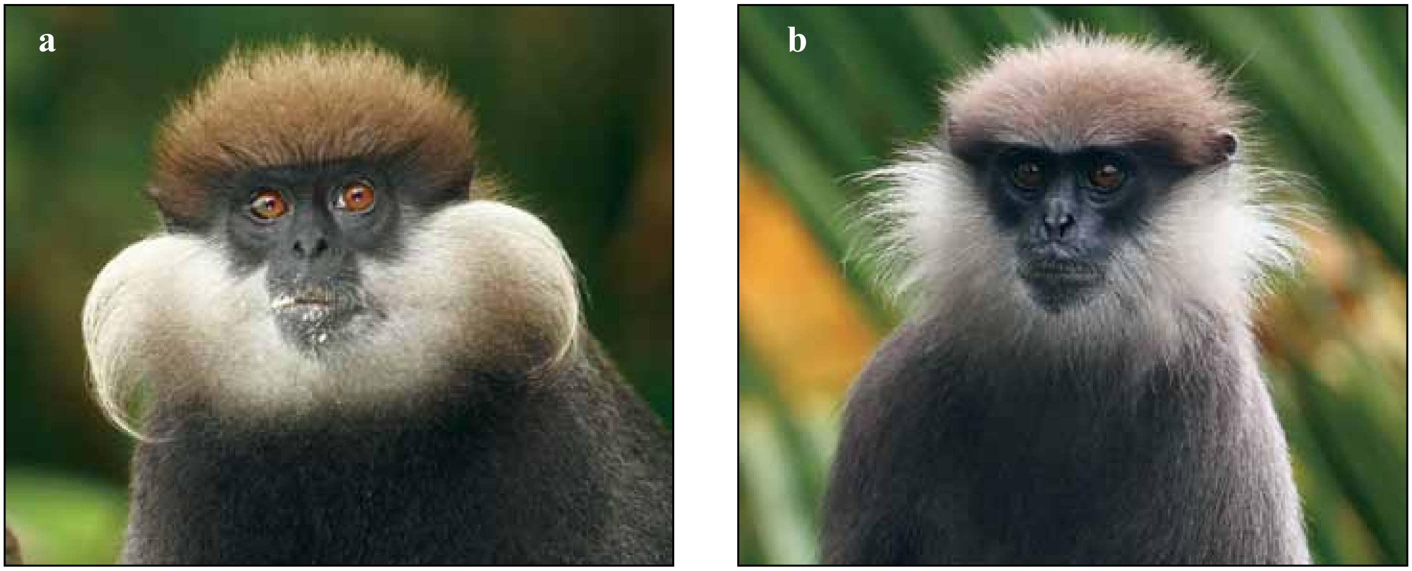

Figure 4. Exemplars of cranial features of the Deniyaya and Getabaruwa troops compared with individuals elsewhere in the southwest study area: a) Getabaruwa troop member showing the characteristic flattened brow line, long and curved whiskers, and darker brown hair crown; and b) a standard specimen of *S. v. vetulus*. Photographs by Nadika Hapuarachchi.

Distributions of the study troops

Although 10 troops were found around the protected area of the Sinharaja Rainforest Reserve (T6, T7, T8, T12, T13, T16, T17, T18, T19, T22), the majority were outside of protected areas. Of the 14 troops containing white color morph individuals, 12 were found in the rainforest, four of them bordering tea plantations; one troop was also found occupying home garden habitat and another was in a mixed habitat home range. Troops containing the white color morph were maximally 18.5 km apart (T16 and T26), very close proximity was found between four troops to the West of Deniyaya (<2 km; T17, T18, T19, T22). One white infant was documented in troop 14, which has a more southerly location compared to other white individuals (Fig. 5). It is possible that this individual was albino as the initial sighting was brief and it has not been seen since 27 September 2011, indicating an early death.

Group composition

Minimum and maximum troop sizes recorded were five to 11 members, with an average troop size of 7.5 (n=26). In total, 30 individuals were recorded displaying the newly documented white color morph: two alpha males, 14 adults of which 13 were females, eight sub-adults, and five infants (Table 1). A single white adult individual could not be sexed and two sub-adults were determined male; all other minors were of unknown sex. The maximum ratio of standard pelage to white was 3:2, the alpha male of troop T18 was of the white color morph (Table 1). Combinations of white mother and white infant (T8 and T19) and white mother with standard-colored infant (T15) were recorded (Figs. 6 and 7). Changes in troop composition (births and deaths) are not analyzed in this paper, although it should be noted that 49 injuries and 33 deaths were caused by electrocution during the study.

Discussion

Limited information is available on the endangered *S. v. vetulus*; our study aimed to augment previous findings, focusing on troop composition and behavioral adaptations within the varied and changing habitat of the southern subspecies. The importance of long-term research has been demonstrated by the extraordinary and unexpected discovery of this new distinct color morph (Fig. 1a). The striking color morph should stir interest beyond the scientific community, across the Biodiversity Hotspot of Sri Lanka (Myers 2000) as a source of national pride in relation to the abundance of endemics the island supports (Crusz 1973; Erdelen 1988). The authorities must begin to cross-reference issues consistently across ministries, for the preservation and protection of known, unknown, and newly discovered flora and fauna.

Different morphological characters, compared to other *S. v. vetulus*, are found in the Deniyaya and Getabaruwa troops, situated predominantly in the rainforest. Smaller body size, a flattened brow shape and longer, more curved whiskers are exhibited by all members of the 13 study troops that contain white individuals (Fig. 4a), excluding the southerly troop 14 with a dead white infant presumed to be albino (Fig. 5). The pelage is different within these troops, not only in the white color morph individuals but also in the standard color morph; the hair is darker on the body and the head crown, and the white pubic patch is also more prominent.

A general darkening of pelage in the Hanuman langur, *Semnopithecus entellus* (Dufresne 1797), is noted in the southern wet zone of India (Pocock 1939; Nag 2011). Coat color is a plastic morphological character in langurs, although other data follow a cline unlike our observed difference in a small group. The two color morphs interbreed freely, producing offspring of either color (Figs. 6 and 7), and a varying degree of

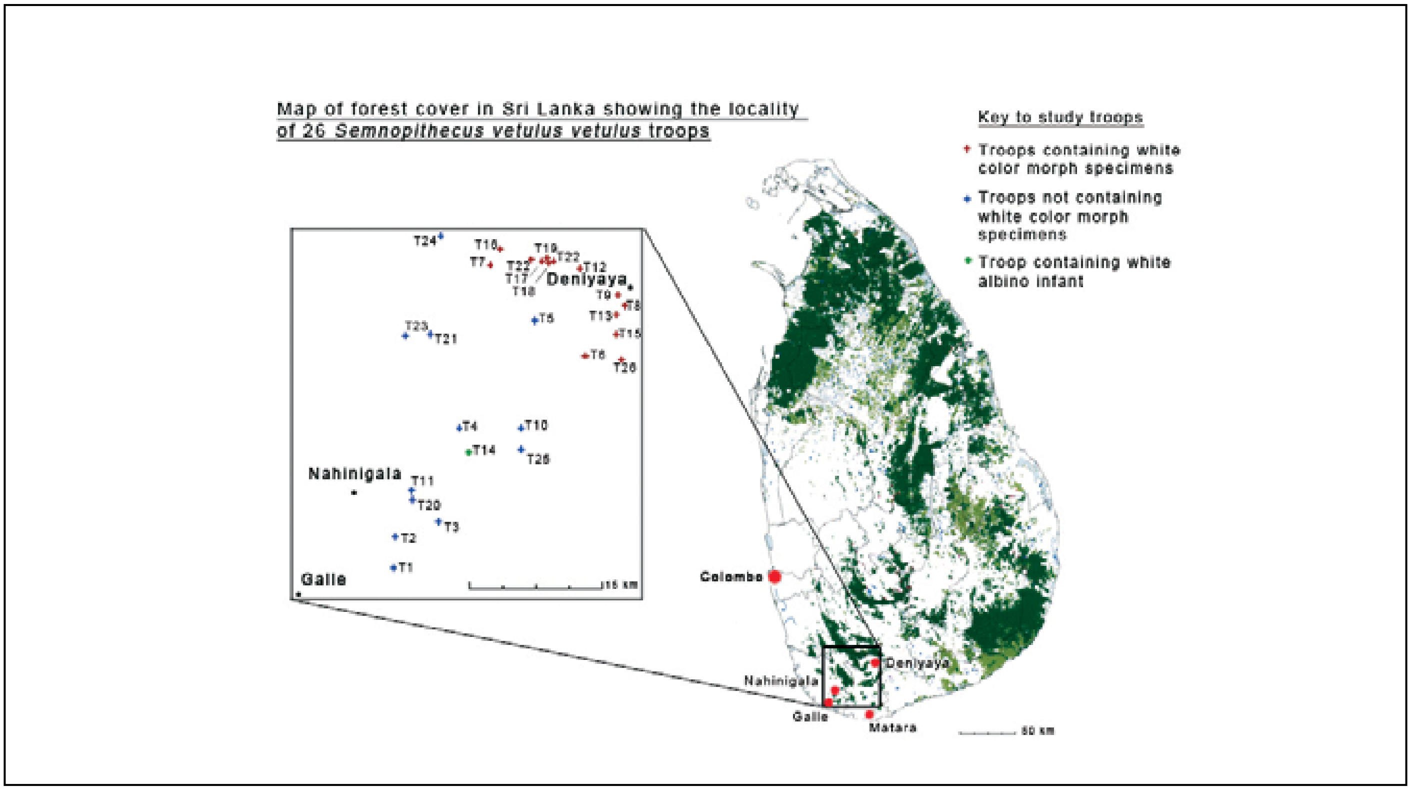

Figure 5. Map of Sri Lanka's forest cover, with an enlargement (inset) of the Galle and Matara districts surveyed by the Wildlife Conservation Society Galle. Red crosses show where troops containing the white color morph are located and blue crosses show the location of troops studied that do not contain the white color morph. The single green cross indicates the troop containing an albino infant. Source of the forest cover data: *Assessment of Tree Resources in the Home Gardens of Sri Lanka* by Ariyadasa (2002).

ashy patches can be seen on the body of the 30 individuals exhibiting the white color morph (Fig. 2). Further investigation and monitoring is required to determine whether genes are dominant-recessive, possible regulatory gene changes, and the possibility of a sexual preference arising.

During a survey conducted by Rudran (2007), interviewees informed of the shooting of six western albinos in 2003, presumably killed for their pelts. The white color morph is still a rarity and requires immediate government protection from poaching. A standard pelage specimen was found shot near the rural villages of Kotapala and Deniyaya in April 2011, which highlights the plea of Dela (2004): culturally related tolerance may not be ubiquitous and should not be relied upon in long-term conservation strategies. A range of fatalities were also found to be induced indirectly by human co-habitation, in congruence with western studies (Dela 2004; Rudran 2007). Mortification from dog attacks or speeding vehicles occurs due to the langur being ill-adapted for ground locomotion (Hladik and Hladik 1972; Moore 2007). A consequential preference to remain above ground results in the use of power lines when crossing roads, which caused 49 injuries and 33 deaths from electrocution recorded by the team during the study. As human population pressures continue to deplete the natural habitat of the langur, fragmentation of the landscape will only exemplify these fatal dangers further.

Only 2% of undisturbed forest remains in Sri Lanka's wet zone, and forest cover declines continuously as just 21% of the remnants are under protection (Kumar 1999). Lowland tea plantations in the south often border rainforest and encroachment may cause further habitat loss for *S. v. vetulus*; plantation agriculture has left the hill country almost devoid of forest except for isolated patches above 1,524 m (Wickramagamage 1998). The resourcefulness of the langur, shown in their exploitation of home gardens (Dela 2007), can also be seen by those bordering tea plantations that are often recorded feeding on *Albizia* (Fabaceae), a non-commercial, imported genus used for tea shade. It is vital that the Southern Province authorities recognize the sheer economic value of high biodiversity in terms of sustained tourism, and implement strict borders and surveillance on forest reserves such as Sinharaja.

Part of the Colombo-Matara Expressway, between Colombo and Galle, was due to open in September 2011. The road will isolate all troops 15–20 km from the coast. The formation of a permanent barrier to gene flow exemplifies the problems of a fragmented habitat to an acute extreme (Parker 2008). The viability of the populations to the west and south of the road is now highly questionable. Troops that inhabit areas already widely affected by the strains of prolific human settlements, radiating from the coastal road, will become genetically isolated from inland troops.

The coastal corridor formed by the Expressway will be separated from the remaining rainforest reserves in the southwest, and a tendency towards home garden and plantation frugivory may also increase as more troops become habituated to humans. The physiological effect of a low diversity diet still requires further investigation (Dela 2007; Moore 2008). The perceptions of the people in the south must now be monitored, as in the west, where langurs are often classified as pests when coexisting in an anthropogenic landscape (Dela 2007; Rudran 2007, Parker 2008). A commensal existence with humans may currently be possible but it is implausible that the tolerance of the Sri Lankan people forms a sustainable plan for conservation (Dela 2004; Nahallage et al. 2008; Parker 2008).

Guidance for future conservation and research opportunities

The conservation of primates in Sri Lanka does not currently hold a priority status; the departments of forestry, wildlife, environment, agriculture, and urban planning all fall into different ministries that rarely cross-reference issues. Although the law in Sri Lanka protects primates, *S. vetulus* faces a perilous future if national policies are not implemented to ensure the species is protected. Guidance for new conservation strategies in the south should be deduced from those for the Critically Endangered western purple-faced langur (IUCN Red List 2011), *S. v. nestor* Bennett, 1833. The status of the western subspecies as one of the 25 most endangered primates in the world (Dela and Rowe 2007) has led to the majority of *S. vetulus* research focusing on this subspecies. Conservation advice that tackles human perceptions of primates in the vicinity of Colombo, the capital city of Sri

Table 1. The 26 troops recorded with the date of first recording, localities, habitat type, total number of individuals, and details of white color morph members.

Troop ID	Date of first recording	Coordinates		Nearest village	Habitat type	No. of members	White color morph individuals
		Latitude	Longitude				
T1	01 May 2007	6°03'38"N	80°19'00"E	Hiyare	HG	5	
T2	29 January 2008	6°05'53"N	80°19'04"E	Kottawa	RF	10	
T3	05 November 2008	6°06'25"N	80°21'38"E	Yakkalamulla	HG	5	
T4	04 May 2009	6°12'14"N	80°23'01"E	Udugama	RF	11	
T5	30 July 2009	6°18'42"N	80°27'35"E	Millawa, Morawaka	RF	10	
T6	02 August 2009	6°16'35"N	80°30'43"E	Getabaruwa, Morawaka	RF	9	1 sub-adult, sex unknown
T7	25 August 2009	6°22'06"N	80°24'54"E	Menikavita, Neluwa	RF	7	1 sub-adult, sex unknown; 1 infant
T8	02 January 2010	6°19'06"N	80°32'38"E	Diyadawa, Deniyaya	HG/RF	6	1 adult female; 1 infant
T9	21 January 2010	6°20'17"N	80°32'41"E	Deniyaya	RF	6	1 alpha male; 1 adult female; 1 sub-adult, sex unknown
T10	19 February 2010	6°12'12"N	80°26'48"E	Pitabeddara	HG	8	
T11	01 March 2010	6°08'21"N	80°19'60"E	Nakiyadeniya	RF/TP	9	
T12	15 April 2010	6°21'52"N	80°30'23"E	Mederipitiya	RF	8	1 sub-adult, sex unknown
T13	07 May 2010	6°19'37"N	80°33'06"E	Diyadawa, Deniyaya	RF	8	1 sub-adult, male
T14	15 May 2010	6°10'42"N	80°23'36"E	Dediyagala	RF	6	1 infant
T15	22 May 2010	6°17'54"N	80°32'39"E	Kotapala	RF/TP	7	2 adult females; 1 adult, sex unknown
T16	15 June 2010	6°23'03"N	80°25'26"E	Warukadeniya	RF	7	1 adult female; 1 sub-adult, male
T17	05 August 2010	6°22'26"N	80°27'23"E	Lankagama	RF	6	2 adult females
T18	18 September 2010	6°22'17"N	80°28'43"E	Wathugala	RF/TP	6	1 alpha male; 3 adult females
T19	19 September 2010	6°22'13"N	80°28'31"E	Lankagama	RF/TP	10	3 adult females; 1 infant
T20	24 September 2010	6°07'49"N	80°20'09"E	Nakiyadeniya	HG	7	
T21	02 October 2010	6°17'56"N	80°21'15"E	Malgalla, Hiniduma	HG/RF	6	
T22	14 October 2010	6°22'18"N	80°27'59"E	Pitadeniya, Lankagama	RF/TP	9	1 adult female; 1 infant
T23	20 October 2010	6°17'46"N	80°19'39"E	Hiniduma	RF	5	
T24	10 December 2010	6°23'53"N	80°21'50"E	Batuwangala, Neluwa	RF	8	
T25	11 January 2011	6°10'52"N	80°26'47"E	Kaduruwana	RF	6	
T26	19 January 2011	6°16'20"N	80°32'55"E	Kotapala	HG	10	2 sub-adults, sex unknown

Lanka, can be used as a case study for other provinces as they encounter similar population pressures (Dela 2007; Rudran 2007; Nahallage 2008; Parker 2008).

Rudran (2007) recently surveyed *S. v. nestor* in the densely populated areas of the west, where 81% of its habitat had been lost due to deforestation. The 21 km² of rainforests around Kalatuwawa and Labugama reservoirs that were identified as the last major strongholds of the western subspecies will now be permanently divided from the population on the other side of the Colombo-Matara Expressway. The initial road route has been altered in congruence with the environmental impact assessment review in order to preserve important wetland systems close to Colombo (RDA 2007). Road construction was also briefly suspended in September, in order for the UN to receive a full report on the impact of the expressway on the Sinharaja Rainforest. Global attention is now on the Sri Lankan government to protect the reserve, although, the international recommendations to expand the protected area are unlikely with the road less than 100 m from the current border. The Southern Transport Development Project has made essential improvements to infrastructure and produced biannual environmental monitoring reports during construction, but the government must now strictly implement the National Wildlife Policy, which was updated in 2000.

The conflict that may arise from primate crop damage, especially in the narrow coastal corridor formed by the road, can be subdued by a systematic quantitative report of agricultural loss due to primates, often perceived to be of a greater extent than in reality (Siex and Struhsaker 1999; Riley 2007; Nahallage 2008). Reports should clearly inform farmers and the general public of the importance of biodiversity in

Figure 6. Offspring from a white mother can be of either color morph: a) white color morph mother with white infant. Photograph by Nadika Hapuarachchi.

Figure 7. White color morph mother with black infant. Photograph by P.A. Rohan Krishantha.

Figure 8. An individual crossing the road using plastic coated wires. Photograph by Nadika Hapuarachchi.

Figure 9. An electrocution fatality due to road-crossing using live wires. Photograph courtesy of Karen Conniff.

terms of how it could benefit themselves and their families in the future. The Sri Lankan culture is focused strongly on religion and family; therefore, a religious overtone should be included in workshops and talks, with the preservation of wildlife directly linked to the prosperity and wealth of future generations.

Semnopithecus v. vetulus is likely to habituate further to humans, becoming an easy target for rifles and catapults (Eschmann 2008), but occurrences such as the shooting we recorded and that of Dela (2004) should stop if the whole community is aware of the consequences. Education of the younger generation is possible through schemes such as 'Trees for monkeys' by the Wildlife Conservation Society Galle, which allows children to plant, for example, an endemic *Artocarpus nobilis* tree (Moraceae). The scheme highlights the importance of conserving non-commercial trees for primate consumption to avoid human-primate conflict in relation to crop damage.

Habitat loss is to some extent preventable and repairable, and forest regeneration programs will be essential to the survival of the endemic langur. The Sinharaja Rainforest Reserve is one of the strongholds for the southwest. With good management, troops that include the white color morph members should proliferate in the vicinity of protected areas. The forestry sector master plan (1995) must be strictly followed if the remaining wet zone forest of Sri Lanka is to be protected. The surveillance of strict borders on reserves and co-operation with the urban planning department are necessary as the Southern province continues to develop. Fines should also be implemented as a deterrent for commercial plantations encroaching on valuable habitat.

Connective corridor strategies would appear to suit *S. v. vetulus* as a predominantly arboreal primate (Rudran 2007), although strategies should be thoroughly investigated in terms of optimal width and effect on other non-target species (Soulé and Gilpin 1991). On a smaller scale, where NGOs and volunteers could contribute relatively inexpensively, rope bridges and lines for crossing to nearby fragments and over roads could reduce genetic flow barriers and mortality by electrocution. Fragmentation outside of protected areas will undoubtedly continue; the viability of small pockets of isolated troops is uncertain (Parker 2008), therefore increasing connectivity can only help in avoiding local extinctions.

Further genetic analysis is required in respect of the 13 troops around Deniyaya and Getabaruwa villages; the morphological differences observed in the field indicate the possibility of a new subspecies. DNA samples retrieved from these troops and other *S. v. vetulus* troops will require meticulous comparison of ample nuclear and mitochondrial markers, as divergence may not be particularly old. In order to implement effective conservation measures the potential sub-specific status of these troops must be determined (Brandon-Jones 2004).

The genetic mutations required for color change have been studied in several mammals, a classic example being rock pocket mice (*Chaetodipus intermedius*; Merriam, 1889); the mc1r gene and regulatory gene Agouti have been pinpointed as color determinants (Hoekstra 2003). Changes in coat color — a plastic morphological character in langurs (Hill 1939; Pocock 1939; Nag 2011) — do not indicate speciation (Fig. 3), although the observed cranial and size differences require further investigation. The present discovery of an unusual new color morph provides research opportunities for population and evolutionary geneticists into a recent and major color alteration, along with the prospect of promoting, protecting, and conserving Sri Lanka's endemic and endangered primate species. The striking white primate will hopefully provide an iconic image for the reinforcement of the current conservation strategies employed, heightening awareness of the vast number of endemics on the island and instilling much needed pride in the Sri Lankan populace regarding the biodiversity of their island.

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Distribution of Rhesus Macaques (*Macaca mulatta*) in Bangladesh: Inter-population Variation in Group Size and Composition

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Abstract: In Bangladesh rhesus macaques (*Macaca mulatta*) are found in forested habitats and urban areas. From 2005 to 2010, we investigated the distribution of rhesus macaques throughout the country. Populations were estimated by line transect, point sampling and direct counting. A total of 37 groups in 16 localities were recorded in urban areas. Overall, group size in urban areas ranged from 22 to 91 individuals, with a mean of 41.3 ± 16.7. Rhesus macaques in urban areas were found mostly near Hindu communities. Nearly five times as many groups (n = 176) of rhesus were observed in the forested habitats of the country. Overall group size in natural habitats varied from 10 to 78 individuals, with a mean of 30.2 ± 10.9. Of the natural habitats, the northeast rainforests were found to support the largest groups (38.9 ± 10.3, n = 49), while smaller groups were found in the central deciduous forests (19.3 ± 4.7, n = 18). The adult sex ratio was higher (1 male to 2.86 females) and the ratio between adult and non-adult (immature) was lower (1 adult to 1.70 non-adults) in natural habitats than was found for the populations in urban areas (1 male to 1.93 females, and 1 adult to 2.11 non-adults). In urban areas, the human-monkey conflict is increasing as competition for resources intensifies.

Key words: Rhesus macaque; *Macaca mulatta*; distribution; population; group size; Bangladesh

Introduction

Bangladesh lies between 20°30' and 26°45'N and 88°01' and 92°41'E. It has an area of 147,570 km² and supports about 160 million people. The country largely comprises the flat deltaic and alluvial deposits of the rivers Ganges, Meghna and Brahmaputra and their tributaries. Hill ranges are found in the northeastern and southeastern parts of the country. April and May are typically hot and followed by the monsoon season in June and July. Winter (November–March) is typically cool and dry. At present about 6% of the country is covered by three types of forest: a) semi-evergreen and evergreen forest in the northeast and southeast hill tracts; b) moist deciduous forest in the central region; and c) the Sundarbans mangrove forest in the southwest. Many tea gardens in the northeast support an abundant population of rhesus macaques (*Macaca mulatta*). Urban areas are densely populated with multistoried buildings. In some urban areas, it is the temples and shrines that are particularly occupied by the monkeys.

Seven species (14 subspecies) of macaques are known in South Asia (Molur *et al.* 2003), and five of them are found in Bangladesh. *Macaca nemestrina*, *M. fascicularis*, *M. arctoides*, and *M. assamensis* occur only in the northeastern and southeastern hill areas. The rhesus macaques are distributed throughout the country. They are synanthropic, thriving in human-altered environments, including urban areas, and play a significant role in the culture and traditions of some communities. Rhesus macaques are non-seasonal breeders and, although some have labeled them "weed species" in recognition of their ability to live in densely populated urban areas (Teas *et al.* 1980; Richard *et al.* 1989; Southwick *et al.* 2005) we recognize this adaptive characteristic as an evolutionary strategy that has allowed this macaque to be among the most widely distributed and successful primates in the world.

Primate populations are being reduced or eliminated in many parts of the world due to habitat destruction, competition for food and space, bushmeat hunting, biomedical research, and the pet trade (Wolfheim 1983; Mittermeier 1986). Published data detailing the distribution and population composition of rhesus macaques in Bangladesh is very limited (Green 1978, Gittins 1980), and largely limited incidental or discontinuous observations in the early 80's (Khan and Ahsan 1981). Intensive surveys, which covered 17 primate habitats in the northeastern and southeastern part of the country, were later conducted by Feeroz and colleagues in the late 1990s (Feeroz *et al.* 1995; Feeroz 2001). The present study aims to describe the current distribution of rhesus macaques in Bangladesh and to discuss the variations in group size and composition among populations in relation to habitat diversity and commensality.

Methods

We conducted 75 field surveys between 2005 and 2010, including 14 field surveys in the northeast, 15 in the southeast, and five in the central part of the country, as well as 15 in the Sundarbans mangrove forests and 26 in urban areas. Three to four days were spent in each field survey, comprising a total of 240 days. Three to five permanent line transects were set at each forest site (Feeroz 2001; Hasan 2003, 2007, 2010). In total, approximately 60% of the forested areas in the country were surveyed in this study. Generally, line transects with modification were used to survey populations in forested areas. Since it was very difficult to perform line transect surveys in the mangrove swamps of the Sundarbans, point sampling was used. In urban areas, total counts were used to survey populations. Double counting was avoided by identifying social groups; comparing group size, composition and visible markings of members (injury, abnormalities or other characteristic morphology). At the same time local people were interviewed regarding their religion, culture and attitude toward the monkeys.

GPS coordinates were noted whenever any group of rhesus macaques was found. Group size and composition were recorded for each group. Group size and composition were verified by repeating the survey at a different time of the day and in different months. We initially used six age-sex classes to characterize macaques: adult male, adult female, sub-adult male, sub-adult female, juvenile and infant. However, it proved very difficult to distinguish sub-adult from juvenile's age-sex in forested areas. Thus, we changed our classification to recognize three classes: adult male, adult female and non-adult (rest of the member of the group as a single category). Vegetation types were categorized as semi-evergreen forest, evergreen forest, deciduous forest, mangrove forest, plantation, tea garden and scrub forest (which include crop fields, scrub-bushes, and bamboo thickets). Urban areas were further categorized into frequent provisioning areas (regular, typically daily or nearly daily) and infrequent provisioning areas (less than once per month).

Results

Rhesus macaque populations in Bangladesh can be divided into two major categories: 1) those living close to human settlements (generally known as urban monkeys); and 2) those living in forested habitats. Mean group size was larger among urban monkeys ($t=2.08$, $p<0.05$).

A total of 37 groups of rhesus macaques were identified among 16 urban populations. All these populations were geographically isolated from each other by 30 to 300 km apart (Fig. 1). The number of groups identified at the urban sites varied from one to five. In urban settings the total population size ranged from 55 to 260 individuals (mean 95.5 ± 62.3, $n=16$) with individual group sizes varying from 22 to 90 individuals (mean 41.3 ± 16.7). In urban areas adult males and adult females comprised 11% and 21% of the populations, respectively, while non-adults comprised 68% of the population (Fig. 2). The average ratio between adult males and adult females was 1:1.93. The average ratio between adults and non-adults was 1: 2.11 (Table 1).

In all, 176 groups were identified in natural habitats. Among these groups 49 were identified in the northeastern region, 68 in the southeastern region, 18 in the central region and 41 in the Sundarbans (southwestern) (Fig. 1). Group size of rhesus macaques in forested habitats varied from 10 to 78 (mean 30.2 ± 10.9, $n=176$) individuals. Among forested sites, the rainforests of the northeastern region supported the largest mean group size (38.9 ± 10.3, $n=49$), while the smallest mean group size was observed in the central deciduous forests (19.3 ± 5.5, $n=18$) (Fig. 3). The adult sex ratio was higher (1 male to 2.86 females) while the ratio between adult and non-adults (immatures) was lower (adult:non-adult = 1:1.70 in natural habitat) than that of the population in urban areas (1 male to 1.93 females and adult:non-adult = 1:2.11) (Table 2). Mean group size of rhesus macaques living in urban areas was significantly larger than that of forested areas ($t=2.08$, $p < 0.05$).

A significant variation ($t=6.7$, $p <0.05$) in group size was also observed among the forested rhesus groups occurring in different habitats—semi-evergreen forest, evergreen forest, deciduous forest, mangrove forest, planted forest, tea garden and scrub forests.

Frequent provisioning was found in seven of the 16 urban sites: Sadhana, Dhamrai, Bormi, Chashnipeer, Syed Jahan, Charmuguria and Chandpur. In these frequently provisioned areas group size ranged from 30 to 90 individuals with a mean group size of 57.85 ± 16.84. In infrequently provisioned areas, group size ranged from 22 to 57 individuals with a mean group size of 32.33 ± 7.17. Group size was significantly larger in the sites where the monkeys were frequently provisioned ($t=5.42$, $p <0.05$).

Discussion

Bangladesh is a densely populated, developing country. At the time of writing this, about 6% of the land area of the country was covered by forests (Gain 2002). Due to increases in human populations and rapid urbanization, the existing forested areas are still facing continuous threats of degradation. In addition to this, human population pressures have accelerated the fragmentation of wildlife habitats, including those of rhesus macaques (Hasan 2003, 2010). Although few data on rhesus ranging patterns are available, research at Lawachara National Park (Feeroz 1999) indicates that a group can range over 5 km², and adult males in the population

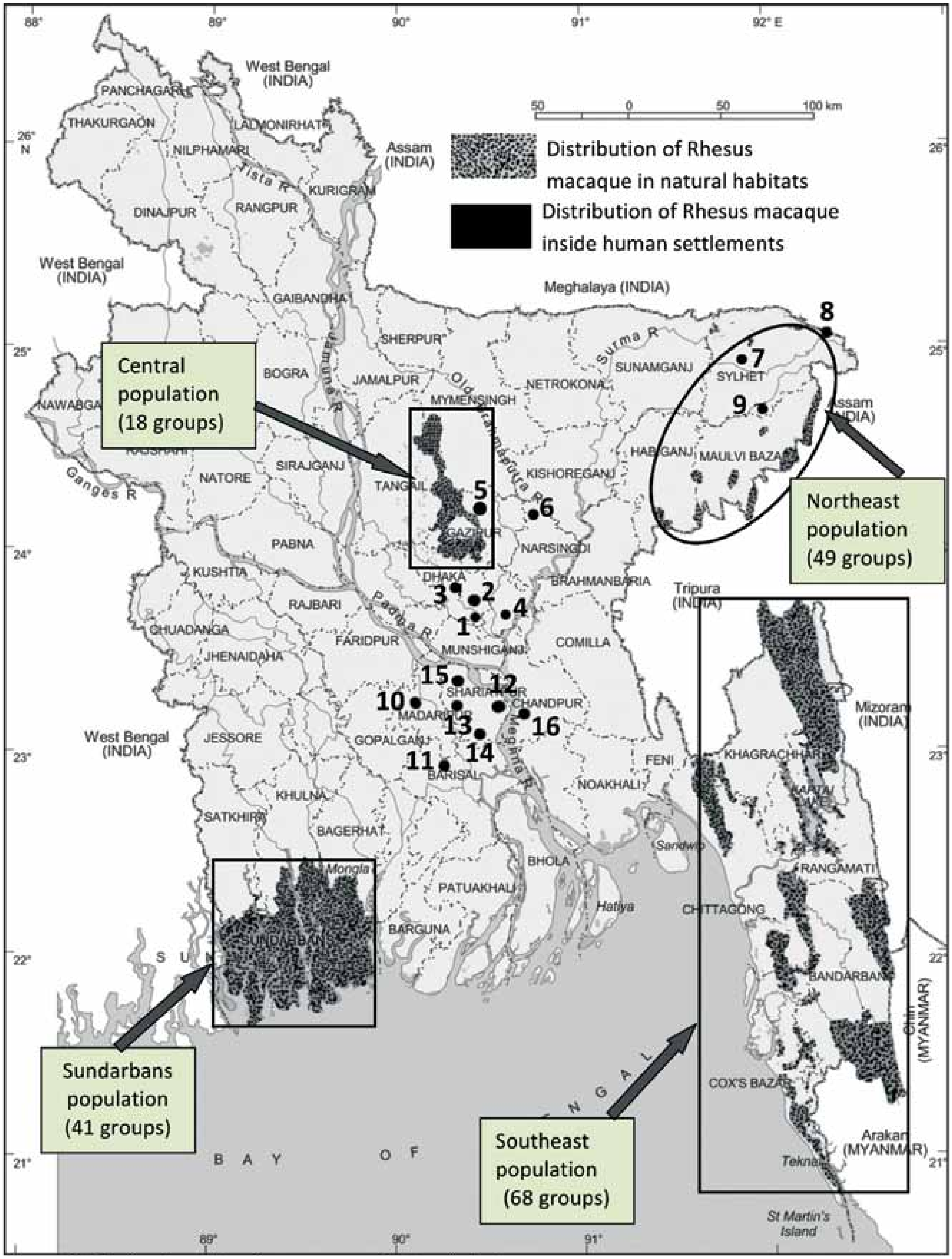

Figure 1. Distribution of the rhesus macaque in Bangladesh. Note: 1- Old Dhaka (4 groups), 2- Dhaka cantonment (3 groups), 3- Dhamrai (2 groups), 4- Narayanganj (2 groups), 5- Bormi (2 groups), 6- Rampur (3 groups), 7- Sylhet town (5 groups), 8- Jointapur (3 groups), 9-Fenchuganj (1 group), 10- Charmuguria (3 groups), 11- Wazirpur (3 groups), 12- Nandanshar (1 group), 13-Kartikpur (1 group), 14- Kolargaon (1 group), 15- Naria (1 group), 16- Chandpur (2 groups).

can move about 10 km in three days, which indicates that adult males may travel about 20 km even in a fragmented habitat. In this situation we considered 40 km as the separator distance between two populations of rhesus macaque in Bangladesh. Koganezawa (1995) considered 15 km as the separator distance between the two populations of Japanese macaque, while several studies recorded male migration of more than 45 km in this species (Yoshimi and Takasaki 2003). Population genetic studies of Japanese macaques suggest that groups geographically separated by more than 100 km are genetically distinct from each other (Nozawa *et al.* 1996). However, from the ecological point of view, several factors may affect male migration, including geographical barriers such as large rivers, large human settlements, and discontinuous habitat.

The largest population and the largest group sizes of rhesus in urban areas were recorded at Charmuguria in the Madaripur district. Due to provisioning by the Government between 2006 and 2009 (Fig. 4), the rhesus population increased very quickly and expanded to Madaripur town, 10 km away from Charmuguria. An abrupt end to provisioning in 2009 led to food scarcity, which subsequently resulted in

Table 1. Rhesus population inside human settlements in Bangladesh.

Urban population		**Population size**	**No. of groups**	**Mean group size**	**Range**	**AM:AF**	**AD:NAD**
Location	**GPS coordination**						
Old Dhaka	23°42.192' N, 90°25.477'E	159	4	39.8±13.8	26–59	1:2.07	1:2.70
Dhaka cantonment	23º49.069'N, 90º24.242'E	92	3	30.7±5.8	24–35	1:1.80	1:2.29
Dhamrai	23°55.056'N, 90°12.637'E	103	2	51.5±4.9	48–55	1:2.22	1:2.55
Narayanganj	23º36.903'N, 90°30.716'E	55	2	27.5±3.5	25–30	1:2.20	1:2.44
Bormi	24°14.669'N, 90°31.301'E	102	2	51.0±5.6	47–55	1:2.00	1:2.09
Rampur	24º14.226'N, 90°43.250'E	81	3	27.0±3.0	24–30	1:2.00	1:2.38
Sylhet town	24°54.314'N, 91°52.418'E	260	5	52.0±24.6	31–84	1:1.97	1:2.02
Jointapur	25º05.930'N, 92°07.768'E	93	3	31.0±9.5	22–41	1:1.83	1:1.82
Fenchuganj	24º39.543'N, 91°58.553'E	57	1	57.0	57	1:1.83	1:2.35
Charmuguria	23°10.249'N, 90°10.036'E	210	3	70.0±20.0	50–90	1:1.88	1:2.04
Wazirpur	22°49.261'N, 90°15.037'E	98	3	32.7±3.8	30–37	1:1.93	1:1.23
Nandanshar	23°17.868'N, 90°28.633'E	33	1	33.0	33	1:1.80	1:1.36
Kartikpur	23°17.732'N, 90°28.737'E	36	1	36.0	36	1:2.00	1:2.00
Kolargaon	23°16.276'N, 90°28.608'E	30	1	30.0	30	1:1.67	1:2.75
Naria	23°18.317'N, 90°24.713'E	36	1	36.0	36	1:1.80	1:1.57
Chandpur	23°13.696'N, 90°38.543'E	83	2	41.5±9.2	35–48	1:1.75	1:2.77
Total/Overall	95.5±62.3	1528	37	41.3±16.7	22–90	1:1.93	1:2.11

Note: AM=Adult male, AF=Adult female, AD=Adult and NAD=Non-adult.

Table 2. Rhesus populations in forested habitats of Bangladesh.

Population	**Population size**	**No. of groups**	**Mean group size**	**Range**	**Adult male: Adult female**	**Adult: Immature***
North East (NE) (Satchari, WBFR, Rema-Kalenga, Adampur, Borolekha, Juri, Harinchara, Khadimnagar and Tea gardens)	1909	49	38.9±10.3	26–78	1:3.43	1:1.36
South East (SE) (Sitakunda, Hazarikhil, Fashiakhali, Himchari, Kaptai, Rangamati, Bandarban and Khagrachari Hill Tracts)	2091	68	30.8±9.8	20–52	1:2.61	1:1.85
Central (Bhawal and Madhupur deciduous forest)	347	18	19.3±4.7	10–26	1:2.56	1:1.93
Sundarbans	966	41	23.6±5.2	14–31	1:2.84	1:1.64
Total/overall	5313	176	30.2±10.9	10–78	1:2.86	1:1.70

Note: * Immature=sub-adult male, sub-adult female, juvenile and infant.

increased human-monkey conflict. Since 2009, local people have reported a considerable increase in the incidents of monkeys biting and scratching people (Hasan 2010).

The smallest group sizes in urban areas were found in Rampur in the Narshindi district. Rampur is located in a rural area with abundant natural vegetation. Rhesus in these areas are not habituated to people and they mostly depend on natural food sources. Rhesus from Rampur are frequently trapped for pet and for performance monkeys, which may contribute to the animal's avoidance of humans.

The Sadhana herbal medicine factory is situated in the heart of old Dhaka city, which is densely populated. There are very few natural food sources near Sadhana, and monkeys are mostly dependent on food supplied by visitors. The herbal medicine factory authority regularly provides food to the monkeys. Although a decade ago rhesus macaques were distributed in 11 areas in Dhaka city (Feeroz *et al.* 1995) currently they are confined to four. The increasing human population is one of the reasons for their population decline. In Dhaka city, monkeys are now limited to Hindu communities, where they range along the walls and roofs of buildings and use utility lines to cross over busy roads. Monkeys climbing onto utility lines are occasionally electrocuted, resulting in burns that are sometimes fatal.

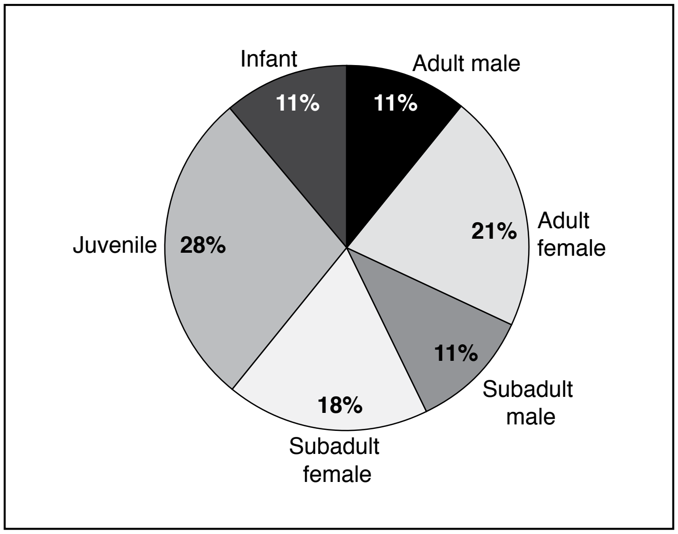

Figure 2. Composition of rhesus populations in different urban areas of Bangladesh.

If we use 40 km as the geographic distance at which gene flow is restricted, rhesus macaques found in the natural habitat in Bangladesh can be divided into four distinct regional populations: 1) northeastern population, 2) southeastern population, 3) central Madhupur population in the central part, and 4) Sundarbans population in the southwest of the country.

The forests of Bangladesh in the northeast region are surrounded by tea plantations. Three sub-populations of rhesus have been identified in this area. Of these, the largest comprised 39 rhesus groups spread over 100 km², extending from the Satchari Forest Reserve to the border area of Karimganj, and including the Rema Kalenga Wildlife Sanctuary, West Bhanugach Forest Reserve, Adampur, Gazipur tea estate, Jhemai tea estate, Borlekha-Juri forests, Madhabkunda forest patches and surrounding tea gardens. Human settlements have fragmented these forest patches, and tea gardens may provide corridors between them. The rhesus groups are separated by less than 10 km, and surrounding tea gardens make male migration possible among them, making them a single sub-population.

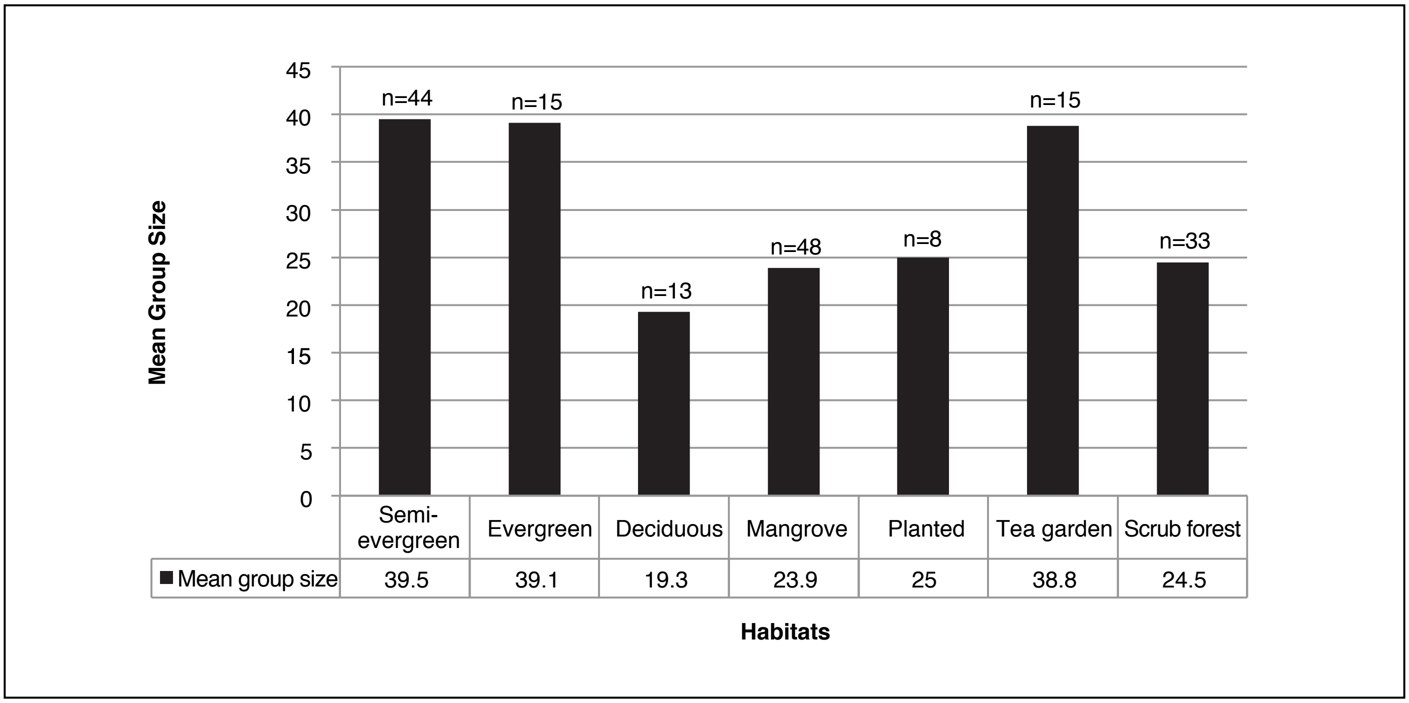

Figure 3. Mean group size of rhesus macaques in different natural habitats.

Two other sub-populations of rhesus were distributed more than 40 km apart from each other, and separated also by large water bodies (locally known as *haor*). The second sub-population (Fenchuganj) comprised six groups of rhesus, ranging in the Fenchuganj-Maijgaon tea estates. The third northeastern sub-population comprised only four rhesus groups ranging in the Malnichara tea estate, the Pathantula villages of Sylhet (Feeroz *et al.* 1995), and the forested areas of Khadimnagar.

The southeastern hill areas of the country support Bangladesh's largest rhesus macaque population: comprising at least 68 groups identified over an area of about 10,000 km² of forests and hills. Evergreen and semi-evergreen forests are more productive than any other forest habitat of Bangladesh, and they provide food for the primates throughout the year (Feeroz 1991, 1999), explaining as such the large group sizes in this area.

Eighteen groups were identified in the Madhupur deciduous forest in the central part of the country. This forest covers about 250 km², with comparatively low habitat fragmentation. Because groups were located less than 10 km apart from each other they were considered to form a single population. Diversity and density of tree species are lower in this forest than in any other forest in the country (Stanford 1991), creating a limited food supply for the macaques during the year. Trees shed their leaves during the winter months, increasing food scarcity during this period. The smaller group sizes observed in Madhupur may be an adaptation to, or result of, low food availability.

Figure 4. Provisioning in an urban area (Charmuguria) by: (a) visitors and tourists, and (b) the government authority. Photos by M. K. Hasan

The mangrove forests of the Bangladesh Sundarbans cover an area of about 6,000 km², and are criss-crossed by numerous rivers and canals. The Rhesus macaque is the only primate species native to the Sundarbans. Forty-one groups were identified there and were considered to make up the southwestern rhesus population of the country. Impermeability of the marshes in the mangroves was a barrier to carrying out more extensive surveys in this region. We considered these groups to be a single rhesus population though some were found in distinct locations more than 40 km from the nearest group.

Female macaques are philopatric, that is, they generally remain in the same group throughout their life. In contrast, males may leave their natal group when they mature. The sex ratio (adult male:adult female) was significantly higher in the forest populations than in the urban populations. This might be due to the restrictions on male migration among urban populations. On the other hand the ratio between adults and non-adults (immature) in urban areas was higher than in the forested populations. Due to provisioning in urban areas by the government, local inhabitants and visitors, the population growth rate is higher than in forested habitats (Hasan 2010).

Rhesus macaques (*Macaca mulatta*) are the most commensal of the non-human primates in many Asian countries such as Afghanistan, Pakistan, India, Myanmar, Nepal, China and Vietnam (Southwick *et al.* 2005). Problems arise when this commensal species becomes a practical competitor with the human population, and Bangladesh is no exception. Rhesus macaques in urban areas generally reside in and around Hindu communities but most of the residents were hostile toward monkeys. Although the Hindu culture venerates monkeys, even Hindus are often hostile toward the monkeys, reflecting the "NIMBY" (not in my back yard) attitude mentioned by Southwick *et al*. (2005).

Increasing conflict between humans and rhesus macaques is a growing problem for both species. In urban areas such as Bormi, Dhamrai, Charmuguria, Chandpur and Chashnipeerermazar (shrine), many people have been badly scratched and bitten by the monkeys. Monkeys destroy their home gardens, fruit trees and crops. On the other hand, monkeys are also beaten, injured and killed by the local people. These types of interactions may increase the risk of bidirectional disease transmission (Jones-Engel *et al.* 2008).

Translocation of rhesus subgroups and groups from urban to rural and forested areas may temporarily appease local human populations but is short-lived and creates problems in the areas of relocation. For the management of the commensal populations, a variety of management techniques such as vasectomies of dominant males, hormonal contraception of adult females, olfactory and taste aversion, noise devices and aggressive dogs have been successful (Southwick *et al.* 2005). We cannot be sure which techniques will be effective in Bangladesh, but the problem needs to be addressed, for the well-being of both of the species.

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Population Density and Abundance of Ebony Leaf Monkeys (*Trachypithecus auratus*) in West Bali National Park, Indonesia

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Abstract: Most of the information available on the conservation status of the ebony leaf monkey (*Trachypithecus auratus*), a species categorized as "Vulnerable" on *The IUCN Red List*, comes from studies conducted in Java. However, these findings may not be representative of other islands of the Indonesian archipelago, such as Bali. In order to estimate the density and abundance of the ebony leaf monkey population in Prapat Agung Peninsula, located in the northern part of the West Bali National Park, Indonesia, we used repeated line transect distance sampling, a standard method for census surveys of wild animal populations, including primates. The estimated group density, individual density, group size, and total population size were 0.95 group/km², 7.11 individuals/km², 7.49 individuals/group, and 422 individuals, respectively. The comparison of these values with those obtained from a previous study conducted 10 years ago in the same area and with the same method showed a marked decrease in population density and abundance as well as changes in the spatial distribution of ebony leaf monkeys. Our data suggest that such trends may be at least partially explained by anthropogenic disturbances, including illegal logging activities and habitat fragmentation. Given these alarming signs, and to better assess trends in the Balinese ebony leaf monkey populations change over time, we urge for the replication of the same survey design in the same study area, at least every five years. Such a survey effort is crucial not only to better understand the socio-ecology of ebony leaf monkeys, but also to determine conservation priorities and devise management plans related to the protection of the populations of this vulnerable primate species in Indonesia.

Key Words: line-transect, distance sampling, group density, ebony leaf monkey, conservation

Introduction

Accurate information on the status and trends of animal populations obtained from inventory and socioecological studies is a prerequisite for successful wildlife conservation programs. In order to test the outcomes of early management initiatives, and then invest further conservation efforts efficiently, wildlife decision-makers need reliable and profitable estimates of density and abundance of animal populations (Goldsmith 1991; Plumptre and Cox 2006). Among the different methods devised to generate such vital information (e.g., Struhsaker 1981a; Brockelman and Ali 1987; Whitesides *et al.* 1988), repeated line-transect distance sampling is considered a relatively simple, rapid, cost-effective, and robust method in terms of accuracy and precision (Burnham *et al.* 1980; Buckland *et al.* 1993, 2001, 2010; Cassey and Mcardle 1999; Barraclough 2000). Line-transect distance sampling proved to be particularly suitable for estimating the density and abundance of forest-dwelling, group-living primates (Defler and Pintor 1985; Chapman *et al.* 1988; García 1993; Peres 1999; Brugière and Fleury 2000; Plumptre and Cox 2006; Marshall *et al.* 2008).

In this sampling method, observers walk along a series of relatively straight transect lines, and record, for each encounter with the study objects, the perpendicular distance(s) from the line to each object detected or to the estimated center of the group formed by all objects detected (Whitesides *et al.* 1988; Hassel-Finnegan *et al.* 2008; Marshall *et al.* 2008). These distances are used to estimate a detection function (i.e. the probability that an object is detected, as a decreasing function of its distance from the line), which, in turn, allows for the calculation of the density of objects (or groups of objects) within the study area, after combining with the encounter rate, defined as the number of objects (or groups of objects) detected per unit length of line (Buckland *et al.* 1993).

Line-transect distance sampling theory is not based on the critical assumption that all objects within a specific area are detected; particularly relevant in forest habitats where the probability of detecting an object decreases rapidly with increasing distance from the observer. According to this sampling method, and with special reference to surveys of forest-dwelling primate groups, the accuracy of the density estimates is based on only four basic assumptions: 1) groups whose centers are located directly over or very close to the transect are detected with certainty (i.e. they are not missed); 2) groups are detected at their initial locations, prior to any movement in response to the observer, and are not double-counted during a census; 3) encounters are independent events; and 4) distances are measured accurately (Buckland *et al.* 1993, 2010).

There are two indigenous non-human primates in Bali, namely long-tailed macaques (*Macaca fascicularis*) and ebony leaf monkeys (*Trachypithecus auratus*) (Brandon-Jones *et al.* 2004). Balinese long-tailed macaques have been extensively studied from an ethnoprimatological perspective and for the management and conservation implications of human and non-human primate interactions, in particular at the tourist site of Pandangtegal Monkey Forest, Ubud (Wheatley 1999; Fuentes and Wolfe 2002; Malone *et al.* 2003; Fuentes and Gamerl 2005; Fuentes *et al.* 2005; Fuentes 2010). In contrast, data on the conservation status of ebony leaf monkeys are scanty.

The ebony leaf monkey (*Trachypithecus auratus*) is a threatened colobine, endemic to the islands of Java, Bali, and Lombok, Indonesia (Weitzel and Groves 1985; Nijman 2000). It is considered Vulnerable due to a past and continued population decline, estimated at more than 30% over the past 36 years (Nijman and Supriatna 2008). Its habitat has largely disappeared due to intensive logging, and its major predator is humans who hunt ebony leaf monkeys for food and commercial purposes (Djuwantoko 1994). This species is listed under CITES Appendix II, and has been protected by Indonesian law since 1999. Little is known, however, about its conservation status in a broad range of natural forest areas (cf. Nijman 2000 for a review). Most of the comprehensive studies have been conducted in a limited number of sites in Java; Pangandaran Nature Reserve (Kool 1989, 1992, 1993; Mengantara and Dirgayusa 1994; Watanabe *et al.* 1996; Mitani and Watanabe 2009), and Gunung Halimun and Ujung Kulon national parks (Gurmaya *et al.* 1994). The findings obtained from studies conducted on the species in Java may not, however, be representative of other islands of the Indonesian archipelago such as Bali (Nijman 2000).

According to Wheatley *et al.* (1993), the West Bali National Park (WBNP) may have the last viable population of ebony leaf monkeys on the island. To our knowledge, the first and only assessment of population density and abundance through line-transect distance sampling and long-term monitoring of home range size in Balinese *Trachypithecus auratus* was conducted about 10 years ago (1999–2000) in Prapat Agung Peninsula, located in the northern part of the WBNP (Vogt 2003). There are no recent data, therefore, on the population density and abundance of ebony leaf monkeys in Bali. Although relevant to socio-ecological studies and conservation issues (cf. Struhsaker 1981b), there is no information on the possible polyspecific association between ebony leaf monkeys and long-tailed macaques. Overall, due to the lack of baseline density estimates on ebony leaf monkey populations in Bali, it is difficult to make accurate inferences about the conservation status and trends of this poorly known species throughout Indonesia.

The goal of this study was to evaluate possible changes in the population density, abundance, and distribution of ebony leaf monkeys in Prapat Agung Peninsula, WBNP, by comparing current data with those obtained 10 years ago by Vogt (2003). Our specific objectives were: 1) to obtain estimates of group density, group size, total population size, and species biomass in the study area by using repeated line-transect distance sampling; 2) to provide a preliminary assessment of the spatial distribution of ebony leaf monkeys in the study area through the comparison of group abundance across the different transects surveyed; 3) to assess a possible (short-term) impact of anthropogenic disturbances on the spatial distribution of ebony leaf monkeys by a) describing the relationship between the presence/location of logging activities and the encounters with ebony leaf monkeys during our transect walks and b) complementing our transect-walk data with transect-drive data collected along the main road built across the park at the southern limit of Prapat Agung Peninsula; and 4) to calculate the rate of mixed-species spatial co-occurrence by quantifying the encounters where ebony leaf monkeys and long-tailed macaques were recorded together.

Methods

Study species

The ebony leaf monkey (*Trachypithecus auratus*), also called the ebony langur, the Javan langur and, in Bahasa Indonesia, "Javan lutung," was elevated as a species from a subspecies of *Trachypithecus cristatus* (Groves 2005). Two subspecies are recognized by Brandon-Jones *et al.* (2004), namely the West Javan ebony leaf monkey (*Trachypithecus auratus mauritius* Griffith, 1821; previously referred to as *T. a. sondaicus*) and the spangled ebony leaf monkey (*T. a. auratus* É. Geoffroy Saint-Hilaire, 1812; previously referred to as *T. a. kohlbruggei*). The study subspecies ranging in the WBNP is *T. a. auratus*.

This Asian colobine has a glossy black pelage, a head-body length of around 55 cm and a tail up to 87 cm long (Weitzel and Groves 1985; Fig. 1). The average body mass (for adult males and females) is 6.2 kg (cf. Fleagle 1999). This diurnal and arboreal primate is mainly folivorous, with a diet consisting primarily of leaves, but also including flowers, buds, fruits, bark, and insect larvae. As is characteristic of colobines, it has a specialized multi-chambered stomach with specific microorganisms in its digestive system to facilitate the breakdown of cellulose and digest plant materials efficiently (Kool 1992, 1993). Thus, this species is able to feed on a substantial amount of foliage, including mature leaves, a food relatively low in nutrients (Kool 1993).

As is typical of many other species in the genus *Trachypithecus*, the ebony leaf monkey lives in groups with a single adult male and a number of immature males, females, and juveniles. Group sizes range from 3 to more than 30 individuals, averaging 17 (Nijman 2000; Vogt 2003). The average home range size is 14 ha, and there is little overlap of the ranges of neighboring groups. Day range lengths vary from about 540 to 740 m (Vogt 2003). Ebony leaf monkeys are found in a wide variety of habitats, including primary, secondary, and remnant forests, rain, evergreen, mixed monsoon, deciduous dry, and mangrove forests, lowland, sub-montane and montane forests, as well as tree plantations and wooded savannah (Kool 1989; Djuwantoko 1994; Nijman 2000; Vogt 2003).

Study site

The West Bali National Park, locally known as Taman Nasional Bali Barat, is located on the north-western side of Bali island, Indonesia, at 8°05'S – 18°15'S and 114°25'E – 114°34'E (Fig. 2). It has an area of 19,366 ha, including the study area, Prapat Agung Peninsula (5,943 ha), which is considered a priority site for conservation in the WBNP. At its southern limit, this peninsula is cut off from the rest of the park by the main Cekik-Teluk Terima road. The park is surrounded by six villages, with a varied ethnic population. It is governed and administered by the districts of Buleleng or Jembrana. Accessibility and land use in the park is bound to a zoning system defining the degree of allowed activities (e.g., agriculture/pastoralism, religion, tourism, education, and research). The park is located in a larger area of protected reserve extending further to the east and covering approximately 77,000 ha, i.e., 10% of Bali's total land area.

The WBNP was created in 1941 with the main goal to protect one the most endangered bird species in the world, the Bali starling (*Leucopsar rothschildi*) and the last wild Indonesian bantengs (*Bos javanicus*), from which most of the Balinese cattle descend. It is now placed under the jurisdiction of the PHPA (Forest Protection Authority Indonesia, Ministry of Forestry). The park has a high biodiversity in a relatively small area, including about 160 species of birds, hawksbill turtles (*Eretmochelys imbricata*), water monitors (*Varanus salvator*), pangolins (*Manis javanicus*), large flying foxes (*Pteropus vampyrus*), black giant squirrels (*Ratufa bicolor*), rusa deer (*Cervus timorensis*), barking deer (*Muntiacus muntjak*), wild boar (*Sus scrofa*), and leopard cats (*Prionailurus bengalensis*). The long-tailed macaque (*Macaca fascicularis*) also occurs there.

Figure 1. An adult male ebony leaf monkey (*Trachypithecus auratus auratus*) in the West Bali National Park (photo by N. Gunst)

The park comprises various habitats, including dry deciduous monsoon forests interspersed with tree plantations, fields, patches of open savannah and, on the coast, mangroves (Vogt 2003; Fig. 2). The dry season lasts from May to September and the wet season from October to April. The average annual rainfall is 1,160 mm, with a range of 972 to 1,550 mm (Vogt 2003). The topography is relatively similar throughout the study site and was unlikely to affect variability in detection distances. Thus line-transect distance sampling was appropriate to assess group density (cf. Buckland et al. 1993).

Data collection

We walked eight transects spread through the study area (Fig. 3). Each transect was 4 km long, except T7 that measured 3.5 km. Each transect was walked 10 times, giving a total distance sampled of 395 km. At least three days separated consecutive censuses of the same transect. Transects T7 and T8 were straight. T1, T2, T3, T4, T5, and T6 followed, at least partially, slightly curved pre-existing trails. Although the use of trails or paths of least resistance as transects for distance sampling was not recommended by Buckland *et al.* (1993, p.18), Hiby and Krishna (2001) argued that the curvature of the trails poses no serious theoretical or practical problems provided the radius of curvature was minimal, and a substantial proportion of detections occurred within the radius of curvature, which was the case in our study. In other words, "the fact that detection distances are generally short in […] forested habitats and that there is a natural tendency for paths and trails to avoid sharp turns suggests that, in terms of curvature, most would be suitable as transects" (Hiby and Krishna 2001: p.730). The only modification required is to record, as the detection distance, the minimum distance from the trail to the target instead of recording the perpendicular distance (Hiby and Krishna 2001).

Accordingly, when recording distances from the transect, we considered the minimum distance for T1–T6 and the perpendicular distance for T7 and T8. However, due to the collection of distance intervals (not exact distances) and the minimum curvature of our transects, it should be noted that 100% of our estimations of minimum distances were identical to perpendicular distances. Therefore, in the following, we refer to these distance measurements as perpendicular distances. We recorded perpendicular distance data by categorizing them into 13 distance intervals, namely 0–5 m, 5–10 m,

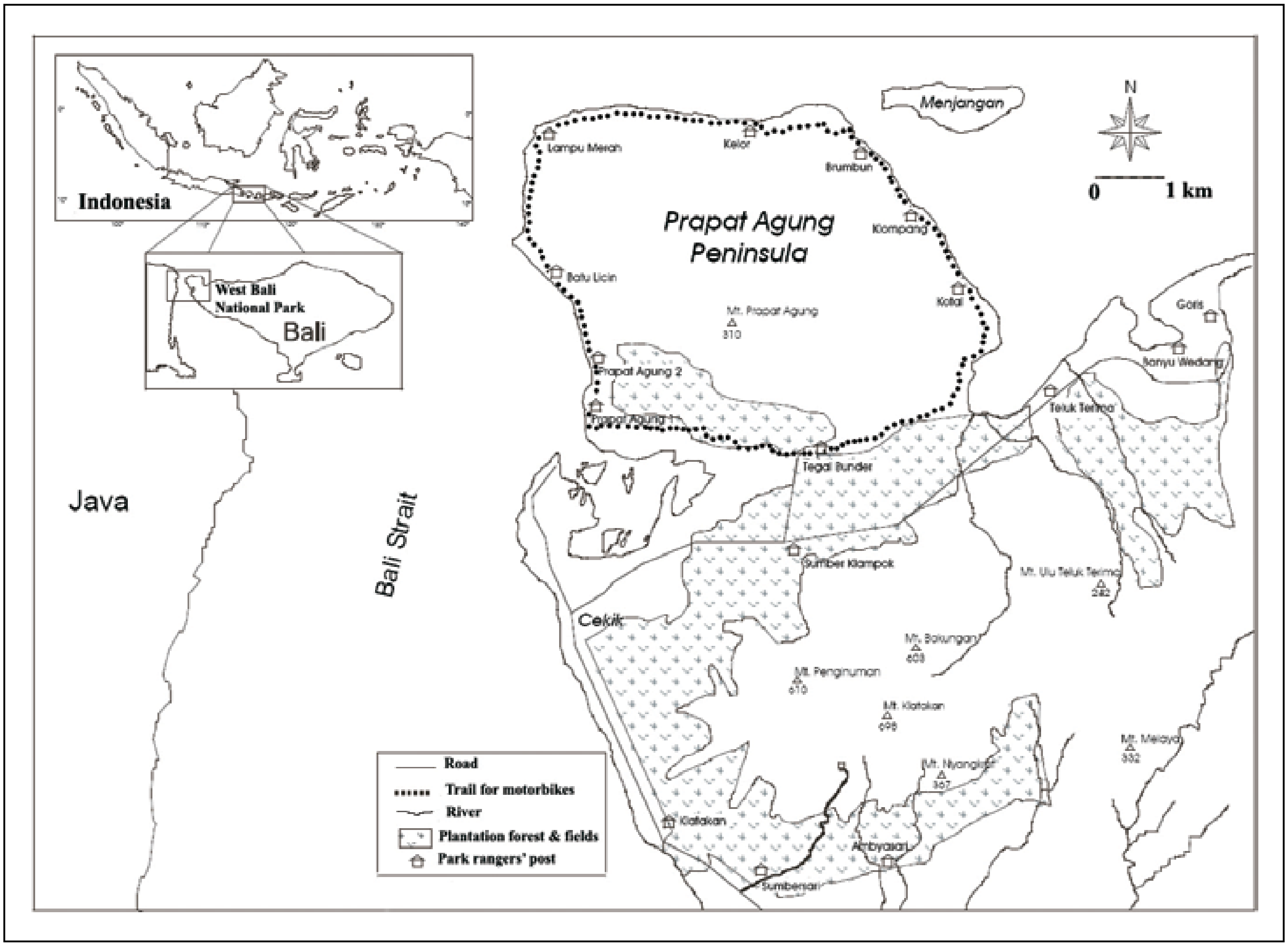

Figure 2. Map of the West Bali National Park, including the study area, Prapat Agung Peninsula (modified from Vogt 2003).

10–15 m, 15–20 m, 20–25 m, 25–30 m, 30–40 m, 40–50 m, 50–60 m, 60–70 m, 70–80 m, 80–90 m, and 90–100 m. To ensure that perpendicular distances would be estimated accurately, observers were trained on evaluating distances by eye prior to the onset of the study, and with the same distance intervals as those used during the study. Data collection started only after they reached 95% of accuracy, when compared these evaluated distance intervals with the distances measured by using a tape.

The survey was conducted by the first two authors (JBL and NG), on a daily basis (except on rainy days) between 06:30 h and 16:30 h, from February to July 2010. During our transect walks, we used the repeated line-transect distance sampling technique, recording the perpendicular distances from the transect line to the estimated center of the groups seen (Buckland *et al.* 1993, 2001). NG walked ahead on the transects, at a constant speed of 1.5 km/h (cf. Ross and Reeves 2003), looking ahead and sideways to detect study subjects, and occasionally using binoculars to determine group sizes. Following 5 m behind, JBL used a pen and paper and a Garmin GPSmap 60CSx to record, for each encounter, the following data: 1) time, 2) GPS coordinates of the detection point on the transect, 3) distance walked from the starting point, 4) the perpendicular distance, estimated by eye, from the transect line to the position on the ground directly under the center of the group of individuals, 5) general information on the (group of) individual(s) detected, such as group size and spread (defined as the largest and smallest diameters of the ellipse occupied by the group, when at least four individuals were detected), and 6) the possible co-presence of long-tailed macaques within 50 m of the center of the ebony leaf monkey group. We also recorded the presence and location of logging, whether current (i.e., taking place during our sampling) or in the past.

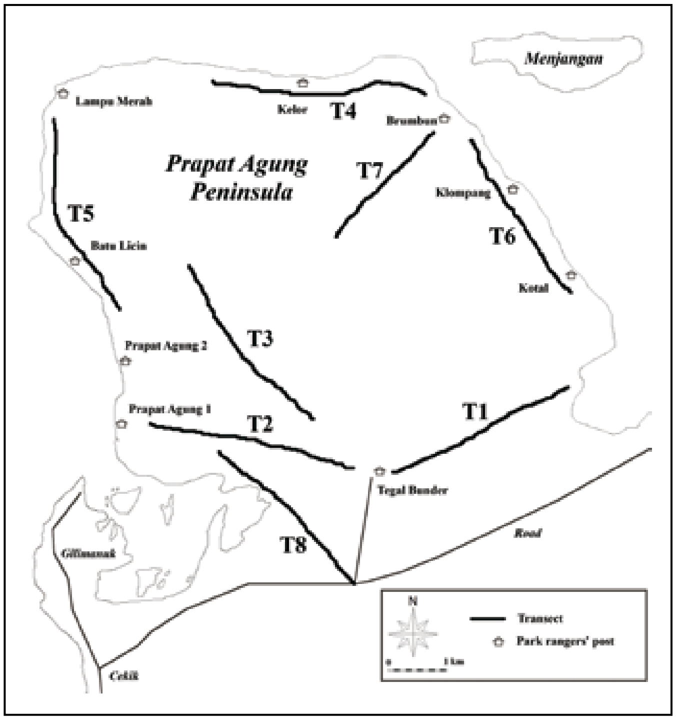

Figure 3. Map of the study area, Prapat Agung Peninsula, including the transects sampled during our survey (modified from Vogt 2003).

The main Cekik-Teluk Terima road traverses the WBNP at the southern limit of Prapat Agung Peninsula. It is lined with plantation forests and fields (Fig. 2), and we complemented our transect-walk data with surveys along this road using a motorbike. These transect drives consisted of repeatedly driving a motorbike along the road at a constant speed of 15 km/h, counting any ebony leaf monkey groups detected on either side. We made ninety one transect drives, each one 12-km long. We recorded the GPS coordinates of each encounter with ebony leaf monkeys. Although we did not use the line-transect distance sampling technique during transect drives, this additional data set gave us a better assessment of the overall abundance and spatial distribution of ebony leaf monkeys in WBNP, by taking into account, not only wild/forest-dwelling groups but also groups living in the vicinity of human settlements and infrastructure.

We recorded a total of 116 encounters during the transect walks and 13 encounters during the transect drives. An encounter was defined as the visual detection from the transect of at least one individual belonging to the study species. The number of individuals seen by the observer during each encounter was referred to as group size. After Marshall *et al.* (2008), we used the term "group" to refer to a cluster/aggregation of ebony leaf monkeys at a given moment in time, and that were located within a maximum of 100 m of each other, which reflects the maximum group spread of this species in the WBNP (Vogt, 2003). In the context of such transect sampling, we were not interested in determining whether the groups we detected were social units or temporary foraging parties/subgroups. This research adhered to the legal requirements of the Republic of Indonesia.

Data analysis

In order to provide estimates of density and abundance of ebony leaf monkeys in the study area, from data collected during transect walks, we used the computer software program Distance 6.0 (Buckland *et al.* 1993, 2001). Our sample of encounters reached the size required by this program, i.e. at least 60–80 encounters for fitting the detection function (cf. Junker *et al.* 2009).

To enter our interval distance data into Distance 6.0, we used the mid-point of each interval, namely 2.5 m, 7.5 m, 12.5 m, 17.5 m, 22.5 m, 27.5 m, 35 m, 45 m, 55 m, 65 m, 75 m, 85 m, and 95 m. We then used the data filter function of Distance 6.0 to match these mid-points with the corresponding intervals. Basic exploratory data analysis showed no particular problems in the data set, such as spiked data, heaping, evasive movement, outliers and possible gross errors. In order to avoid extra adjustment terms that might otherwise be needed to fit a long tail to the detection function (cf. Buckland *et al.* 2001, pp.151–278 153), we truncated distance data prior to analysis. We examined the distribution of distances and, even though a few groups had been detected as far as

90–100 m, we decided to use a 50 m right truncation (i.e., all observations beyond 50 m were discarded). After discarding the corresponding 6% of our observations (in agreement with the 5–10% recommended by Buckland *et al.* 2001; Thomas *et al.* 2010), 109 encounters were considered in the analyses performed by Distance 6.0.

We tested the following four combinations of regular and efficient detection function models (cf. Buckland *et al.* 1993; Thomas *et al.* 2010): 1) uniform key with cosine adjustments; 2) half-normal key with cosine adjustments; 3) half-normal key with Hermite polynomial adjustments; and 4) hazard-rate key with simple polynomial adjustments. To select the type of detection function model that best fit our data set, we used the following series of criteria (cf. Buckland *et al.* 1993, 2001; Thomas *et al.* 2010): 1) the smallest Akaike's Information Criterion (AIC) value; 2) the smallest ratio of the χ^2 goodness of fit statistic divided by its degree of freedom; 3) a few parameters to avoid large bias but not so many that precision is lost (i.e. the principle of parsimony); 4) a Delta AIC = 0; and 5) no warning messages displayed by the analysis engine. From this screening, we selected the half-normal key with cosine adjustments over alternative models.

To consider the survey effort, we used the multiplier function of Distance 6.0 to divide the density estimate by the number of visits per transect (i.e., 10 for each of the eight transects walked). The effective strip width (μ) was defined as the distance from the line at which as many groups were detected beyond μ as were missed within μ of the line (Buckland *et al.* 2001). To estimate group size, we used the mean of observed groups. Variances of encounter rate and group size were estimated analytically/empirically. The encounter rate was defined as the number of groups detected per unit length of transect, i.e., per kilometer walked (excluding those whose centers were further from the line than the truncation distance). The average distance between two consecutive encounters was the difference between two consecutive distances walked from the starting point, as measured from GPS coordinates at each encounter. Precision of estimates was measured in different ways depending on the type of analysis performed: Standard Deviation (SD), Standard Error (SE), Percentage of Coefficient of Variation (%CV, i.e., standard deviation as a percentage of the mean), or 95% Confidence Interval (95% CI).

Results

Group/individual densities, group size, total population size, and species biomass

From the detection function model that best fitted our data (half-normal key with cosine adjustments), we plotted the detection function, superimposed on the histogram showing the detection probability as a decreasing function of the distance from the transect line to the objects detected (Fig. 4). The chi-square goodness-of-fit test gives a measure of how well the model fit the data, based on a comparison of the observed and expected frequencies of observations within the distance intervals. According to Buckland *et al.* (1993), a significant goodness-of-fit statistic is a useful warning that the model might be poor, or that an assumption might be seriously violated. In contrast, our result (χ^2 = 3.22, df = 5, P = 0.666) showed that the model selected fit our data well.

The detection function allowed for the calculation of a series of statistical values (Table 1), which taken together, characterized our line-transect distance sampling survey. Table 1 shows the main estimated values for our study of the

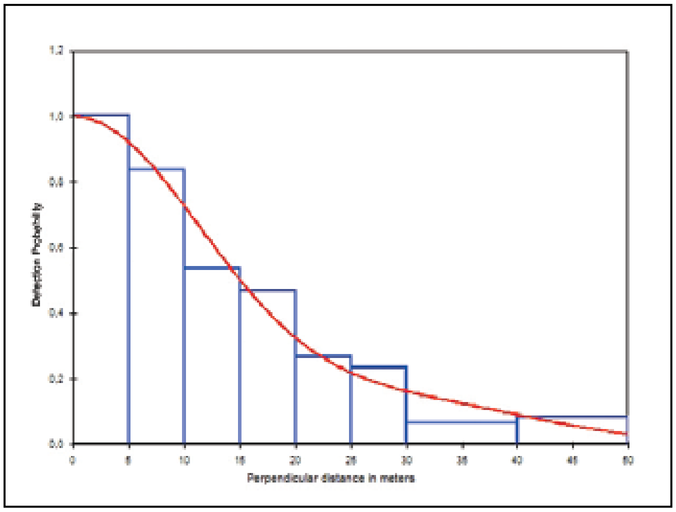

Figure 4. Histogram showing the detection probability as a function of the perpendicular distance from the transect line (interval distances), as generated by the analytical program Distance 6.0, and after right truncation distance set at 50 m. The curve represents the detection function obtained with the detection function model that best fit the data.

Table 1. Estimated values related to the population density and abundance of ebony leaf monkeys in Prapat Agung Peninsula, as obtained from Distance 6.0. Parameters were f(0): probability density function of observed distances evaluated at 0 m, ESW: effective strip width (in meters), ER: encounter rate, DS: estimate of density of groups (number per km²), D: estimate of density of individuals (number per km²), E(S): estimate of expected value (mean) of group size, and N: estimate of number of individuals in the study area. Precision measurements were SE: standard error, %CV: coefficient of variation (i.e. standard deviation as a percentage of the mean), df: degree of freedom, and 95% CI: 95% confidence interval.

Parameter	Estimate	SE	%CV	df	95% CI	
f(0)	0.55E-01	-	10.05	107	0.45E-01	0.67E-01
ESW	18.25	-	10.05	107	14.96	22.26
ER	0.35	-	9.87	79	0.28	0.42
DS	0.95	0.13	14.08	-	0.72	1.25
D	7.11	1.09	15.37	-	5.26	9.60
E(S)	7.49	0.46	6.17	108	6.63	8.47
N	422	64.87	15.37	-	313	571

population density and abundance of ebony leaf monkeys in Prapat Agung Peninsula, including the probability density function of observed distances evaluated at 0 m, the effective strip width, the encounter rate, the density of groups, the density of individuals, the mean group size, and the number of individuals in the study area. Based on the total population size estimate (422 individuals), the mean body mass (6.2 kg; cf. Fleagle 1999), and the surface area of Prapat Agung Peninsula (59.43 km²), the ebony leaf monkey biomass estimate in the study area was 44.02 kg/km².

Spatial distribution of ebony leaf monkeys in Prapat Agung Peninsula

Table 2 shows the group abundance and size in the different transects sampled. This preliminary assessment of the spatial distribution of ebony leaf monkeys within the study area showed similar numbers of group encounters and group sizes in most transects (total average: 0.35 group detected/km), except T1 with relatively high values (0.65 group detected/km), and T3 with relatively low values (0.10 group detected/km). Groups were not only notably separated in space (overall mean distance between two consecutive groups = 1.11 ± 0.78 km; cf. Table 2) but also highly clustered, with 80 out of 96 encounters (i.e., 83.3%) showing group spreads between 20 and 50 m in diameter. The maximum group spread was 100 × 80 m, for only two encounters.

Impact of anthropogenic disturbances on the spatial distribution of ebony leaf monkeys

During our transect walks, we recorded 26 spots where there was active or past logging. They were all in the southern part of Prapat Agung Peninsula (four spots on T1, eight on T2, nine on T3, and five on T8). Nineteen were active and seven showed signs of logging at least several weeks before our observations. Logging significantly decreased the encounter rate (Mann-Whitney U test: $z = 4.94$, $p < 0.001$). We never found ebony leaf monkeys within 1.5 km of places which were being logged, whereas we recorded 11 encounters within 0.1 km of spots where there had been logging in the past.

In the motorbike censuses, we saw ebony leaf monkeys 13 times. The sightings were highly clustered in a 220-m-long stretch along the Cekik-Teluk Terima road, half-way between Cekik and Sumber Klampok (cf. Fig. 2). Unlike elsewhere along the road, this stretch had large trees with stout branches extending over the road, which suggests it may be a dispersal corridor between two parts of a group's home range separated by agricultural fields and pastoral areas. Based on individual observations, and given the little overlap of home range found in these ebony leaf monkeys (cf. Vogt, 2003), we believe that these encounters were all of the same social group.

Rate of mixed-species spatial co-occurrence

One or a group of long-tailed macaques was found within 50 m of one or a group of ebony leaf monkeys 12 times in 116 encounters (twice on T1, seven times on T2, twice on T4, and once on T5), i.e., a rate of mixed-species spatial co-occurrence of 10.3%. In all cases, the long-tailed macaques were on the ground, whereas the ebony leaf monkeys were in the trees. In three encounters (one during a transect walk, which was not considered in our distance analyses, and two during reconnaissance walks), long-tailed macaques gave alarm calls as we approached, which resulted in ebony leaf monkeys moving away from us. We saw no other types of interaction between the two species.

Table 2. Number, mean, and relative location of groups and individuals detected in the different transects sampled, with their corresponding types of vegetation (DDMF: dry deciduous monsoon forest, MG: mangrove, PF: plantation forest, SV: savannah).

Transect	Vegetation	Length (km)	No. of visits	Total number of groups detected (cumulative over visits)	Mean number of groups detected/km	Total number of individuals detected (cumulative over visits)	Mean ± SD (min-max) number of individuals detected per group	Mean ± SD (min-max) number of individuals detected per transect walked	Mean ± SD (min-max) distance (km) between two consecutive groups
T1	DDMF/MG/PF	4	10	26	0.65	240	9.2 ± 7.2 (1–28)	26.7 ± 21.2 (5–64)	0.72 ± 0.36 (0.41–1.55)
T2	DDMF/MG/PF	4	10	13	0.33	107	8.2 ± 4.9 (1–20)	15.3 ± 6.5 (8–24)	1.42 ± 0.83 (0.42–2.54)
T3	DDMF/PF	4	10	4	0.10	24	6.0 ± 3.6 (1–9)	6.0 ± 3.6 (1–9)	n/a
T4	DDMF/MG/SV	4	10	19	0.47	115	6.1 ± 3.1 (1–12)	14.4 ± 9.1 (5–29)	1.17 ± 0.64 (0.43–2.57)
T5	DDMF/PF	4	10	12	0.30	68	5.7 ± 4.8 (1–17)	7.6 ± 6.6 (2–20)	0.52 ± 0.03 (0.50–0.55)
T6	DDMF/MG/SV	4	10	12	0.30	86	7.2 ± 2.9 (3–13)	10.7 ± 4.4 (4–17)	1.31 ± 0.86 (0.71–2.83
T7	DDMF/SV	3.5	10	12	0.34	107	8.9 ± 3.5 (5–15)	13.4 ± 7.5 (6–28)	0.94 ± 0.60 (0.40–1.66)
T8	DDMF/MG/PF/SV	4	10	11	0.28	70	6.4 ± 1.4 (5–9)	10.0 ± 4.5 (5–15)	2.44 ± 1.25 (0.58–3.19)
Total		31.5	10	109	0.35	817	7.5 ± 4.8 (1–28)	13.6 ± 11.4 (1–64)	1.11 ± 0.78 (0.40–3.19)

Discussion

Validity of our line-transect distance sampling design and analysis

Theoretically, it is preferable to sample a series of randomly distributed transects within a given survey area, rather than along pre-existing trails. A permanent human presence may affect the animals' behavior and spatial distribution, and consequently animal density estimates may be biased (Buckland *et al.* 2010). Although we were completely aware of these recommendations in terms of survey design before selecting our transects (two straight transects and six that followed slightly curved pre-existing trails), we emphasize two arguments in support of our methodology.

First, the shape of the detection probability histogram (Fig. 4) suggests that, although several transects were placed along pre-existing trails, a relatively high proportion of encounters occurred directly on or near to the transects (perpendicular distance: 0–5 m), and animals did not always move away from the approaching observer. Second, in practice, non-randomized designs, including transects along pre-existing trails, are frequent in primate surveys (Hiby and Krishna 2001; Buckland *et al.* 2010). As long as the number of these transects is sufficient with regard to the survey region, the design remains acceptable (Buckland *et al.* 2001). In this respect, we claim that, given the relatively small size of the study area, the number of transects (i.e., eight) was sufficient to ensure that they did not pass through areas with atypical densities. Moreover, our transects were widely distributed and regularly spaced.

It may also be argued that laying transects along pre-existing trails means that the habitat might not be sampled in a representative manner, because such trails are often placed either on ridges or along waterways, and thus over- or under-sampling some habitats. In response to this argument, we claim that all the types of habitats present on Prapat Agung Peninsula were sampled by our transects (cf. Table 2), which were therefore representative of the entire study area. Our survey design provided a good coverage of the study area, which increases the accuracy and precision of estimates.

We believe that our sampling conditions did not violate any of the four key assumptions on which distance sampling methods rely (cf. Buckland *et al.* 2001). First, owing to the large size of ebony leaf monkeys and the relatively large number of individuals per group, we were very unlikely to miss groups located directly over the transects. Second, in the vast majority of cases, we were cautious enough not to make the study subjects move away before we detected them in their initial positions. Moreover, our line transect design and our average walking speed (faster than the animals' travel speed) prevented us from possible double counts. Third, our result on the average distance between two consecutive encounters (cf. Table 2) is consistent with the small home range overlap that Vogt (2003) reported for this species, and strongly suggests that our encounters were independent events. Fourth, due to pre-study training, observers were unlikely to introduce biases related to distance measurement errors.

Finally, during our survey, we obtained well over the minimum number of detections (i.e., 60–80) necessary for fitting the detection function (Barraclough 2000). Our testing of different combinations of possible detection function models and subsequent adjustments provided very similar estimates, which is an additional guarantee of high quality survey information. Overall, we believe our survey design and data on the abundance of ebony leaf monkeys in Prapat Agung Peninsula, West Bali National Park, were of sufficient quality to produce reliable estimates of their density in the study area.

Group/individual densities, group size, total population size, and species biomass

In order to evaluate possible changes in the population density, abundance, and distribution of ebony leaf monkeys in Prapat Agung Peninsula, WBNP, we compared our results with those obtained from the only previous survey on this species, in the same study area, conducted 10 years before (1999–2000), and through repeated line-transect distance sampling (Vogt 2003). All the estimated values provided by the current study were markedly lower than those found by Vogt (2003): 1) the estimated group density was 0.95 groups/km² in 2010 versus 1.94 groups/km² in 2000 — a 51% decrease; 2) the estimated individual density was 7.11 individuals/km² in 2010 versus 33.23 individuals/km² in 2000 — a 79% decrease; 3) the estimated number of individuals on Prapat Agung Peninsula was 422 individuals in 2010 versus 1,972 in 2000 (calculated from Vogt 2003, with a study area of 59.43 km²) — a 79% decrease; 4) the estimated group size was 7.49 individuals/group in 2010 versus 17.13 in 2000 — a 56% decrease; and 5) the estimated ebony leaf monkey biomass was 44.02 kg/km² in 2010 versus 191.42 kg/km² in 2000 — a 77% decrease.

We acknowledge that we may have underestimated the individual density, because the group size estimates found from our transects (7.49 individuals/group) underestimated by 56% the mean group size found for this species, based on a long-term monitoring of 13 groups (mean: 17.13 individuals, range: 3–30; cf. Nijman 2000; Vogt 2003). This difference is consistent with other studies showing that the line-transect sampling method systematically underestimates the mean group size of forest-dwelling monkeys because of relatively poor visibility (Green 1978; Defler and Pintor 1985; Simmen *et al.* 1998; Brugière and Fleury 2000). This discrepancy simply suggests that much caution is required when discussing results on group size obtained from distance surveys. They should be regarded as preliminary, and further supported with long-term follows of particular groups (Plumptre and Reynolds 1994; Brugière and Fleury 2000; Plumptre 2000). One advantage of distance sampling, however, is that the estimation of population density can still be accurate even when only a relatively small percentage of individuals (possibly as few as 10–30%) are detected within the sampled area (Barraclough 2000).

It may also be argued that our study period (during the wet season) could at least partially explain our lower values. First, group sizes of ebony leaf monkeys in Java vary according to the climatic conditions of the area, with smaller groups found in areas where the wet season is more pronounced (Nijman 2000). Second, there is no doubt that visibility during the wet season is not as good as it is during the dry season. Seasonal variation in visibility is not likely to account for such differences, however, because the line transect survey by Vogt (2003) was also conducted during the wet season. Moreover, although visibility can be assumed to affect the assessment of individual density more than the assessment of group density, there was also a marked difference between the estimated group densities found in the two surveys.

Overall, the direct comparison of our current data with findings obtained 10 years ago in Prapat Agung Peninsula with the exact same method leads to the conclusion that there has been a significant decrease in the population density and some changes in the spatial distribution of ebony leaf monkeys. The individual density found in our study is also lower than that found in different sites in Java, which range from 20 to 75 individuals/km² (Supriatna *et al.* 1988; Nijman and van Balen 1998; Nijman 2000). It should be noted, however, that these sites tend to be selected because of the local relative abundance of ebony leaf monkeys, which suggest that a more typical density may be in the lower range (Nijman 2000).

Spatial distribution of ebony leaf monkeys in Prapat Agung Peninsula

The comparison of group abundance across the different transects surveyed (Table 2) suggests that the spatial distribution of ebony leaf monkeys in Prapat Agung Peninsula was not entirely uniform. This result may, at least in part, be explained by the impact of anthropogenic disturbance (see below for details). Our results on intergroup distances and group spread were consistent with previous findings for this species, showing highly clustered groups with little home range overlap (Vogt 2003).

Regarding the comparison of the spatial distribution over time, it should be noted that the results obtained by Vogt (2003) were drawn from five transects (T1, T2, T3, and T4 were similar to those sampled in our study, whereas Vogt's fifth transect was in the central peninsula, between T3 and T7). When comparing the mean number of groups detected per km of transect, we found marked differences for T1 and T3, and similar values for T2 and T4: 1) 0.65 groups/km was detected on T1 in 2010 versus 0.05 groups/km in 2000, 2) 0.33 groups/km was detected on T2 in 2010 versus 0.27 groups/km in 2000, 3) 0.10 groups/km was detected on T3 in 2010 versus 0.20 groups/km in 2000, and 4) 0.47 groups/km was detected on T4 in 2010 versus 0.46 groups/km in 2000. The WBNP may have the last viable population of ebony leaf monkeys in Bali (Wheatley *et al.* 1993). The species might also be present, however, in the park's eastern extension and the mountainous interior of Bali island (Nijman 2000).

Impact of anthropogenic disturbances on the spatial distribution of ebony leaf monkeys

Although our preliminary data would need to be supported by a larger sample collected over a several-year period, they suggest a negative effect of logging activities on the presence of ebony leaf monkeys in the vicinity. However, as suggested by their presence around past logging sites, this effect seems temporary, and the monkeys are likely to re-occupy logged areas after a certain delay that remains to be determined by a long-term study. This is consistent with previous research showing that the dynamics of re-occupation of logged areas by most primates is generally slow (Chapman *et al.* 2005). Our finding of the occasional presence of usually cryptic ebony leaf monkeys along a main road with heavy traffic and lined with plantation forests and agricultural fields emphasizes the need to preserve dispersal corridors for this threatened species living in such a fragmented habitat. The main threats currently faced by the Balinese ebony leaf monkeys are continuing habitat loss, degradation, fragmentation, as well as indirect negative impacts from illegal hunting for the Bali starlings (Vogt 2003). Although this species is able to cope with a certain degree of habitat disturbance, some populations may find themselves cornered in small forest remnants, with no possibilities to leave, because of the absence of dispersal corridors and adjacent forest patches (Nijman 2000). In the longer term, the population of ebony leaf monkeys ranging in Prapat Agung Peninsula may face a risk of genetic isolation from other populations in Bali.

Rate of mixed-species spatial co-occurrence

Although line-transect sampling is not typically used to quantify primate polyspecific associations, our data show that ebony leaf monkeys and long-tailed macaques can be spatially associated. The non-negligible rate of co-occurrence, the distinct vertical distribution of the two species, and the few instances of anti-predator benefits for ebony leaf monkeys are reminiscent of true polyspecific associations, defined as associations between two or more species that involve behavioral changes by at least one of the participating species (Strier 2003). More data from long-term group monitoring are needed, however, to clarify whether such co-occurrence was a matter of chance or the result of a true polyspecific association.

Future directions

Overall, this project provided new, broad, and accurate information on the density, abundance, geographical distribution, and ecology of ebony leaf monkeys in Prapat Agung Peninsula, WBNP; data that are necessary to assess the current status of this species, implement conservation priorities, and create management plans for the *Trachypithecus auratus* populations on a larger scale. We believe the comparison of our demographic, geographical, and ecological data with findings obtained in Java (Kool 1989, 1992, 1993; Gurmaya *et al.* 1994; Mengantara and Dirgayusa 1994; Watanabe *et al.* 1996; Mitani and Watanabe 2009) will contribute to provide a comprehensive assessment of the conservation status of *Trachypithecus auratus* in Indonesia.

We hope that: 1) our geographic database will be considered by park managers and other researchers in their decision-making for a better protection of the species and a more accurate assessment of the species' conservation status; 2) our results on the occurrence of illegal logging in Prapat Agung Peninsula will be used by the park authorities to prevent, as far as possible, such a detrimental impact; and 3) our findings will provide a baseline for future replicable census surveys of ebony leaf monkeys in the same area. Providing accurate descriptions of this species' status and demographic trends, long-term inventory studies are crucial for the decisions of wildlife managers in ways of preventing such population decrease tendencies. Our quantification of the precision of abundance estimates may also allow the comparison of our results with those obtained from alternative census methods, such as complete count surveys or methods combining point census and group follows (Harcourt and Fossey 1981; McNeilage *et al.* 2001; Hanya *et al.* 2003).

In the foreseeable future, several focused studies could be conducted in the WBNP, as a direct follow-up on the current research/conservation survey. We suggest four main directions for future efforts devoted to the monitoring of the population of ebony leaf monkeys in the WBNP. First, to assess trends in rates of population change over time, we urge for the replication of the exact same survey design at least every five years. Second, to evaluate seasonal variation in the distribution/movements of ebony leaf monkeys, our findings should be compared with those obtained from an identical survey that would be conducted during the dry season.

Third, to estimate how the population size may be affected by environmental or anthropogenic factors, future studies should stratify the study area (or the entire WBNP) and conduct distinct line-transect sampling within each major habitat type (plantation forest, secondary forest, savannah, human settlements, agricultural/pastoral areas, roads, etc.). Such anthropogenic factors include the subsistence activities of local villagers living inside the park, religious activities (e.g., Hindu gatherings in local temples located in the park), and tourist activities (e.g., guided-tours) on Prapat Agung Peninsula. Our preliminary data suggest that the occurrence and prevalence of illegal logging should be considered in these analyses. Fourth, to assess the population genetic structure of Balinese ebony leaf monkeys, DNA analysis could be conducted from the fecal samples collected in different groups. In the long term, information on genetic variation within and between groups, particularly on a small island such as Bali, could be used to assess the viability of the populations studied (Frankham 1996). Such survey efforts are crucial not only for a better understanding of the socioecology of ebony leaf monkeys, but also to determine conservation priorities, devise management plans, and diversify local education programs related to the protection of the populations of this vulnerable primate species in Indonesia.

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Dr. Annie Gautier-Hion (1940–2011)

The primatology community recently lost one of its most important contributors, taken away by the illness against which she fought for two years. Dr. Annie Gautier-Hion studied central African primates in the field for 35 years. She was best known for her pioneering work on the ecology, evolution and biogeography of guenons, and for a study of western lowland gorillas in Odzala-Kokoua National Park. She contributed greatly to the field of primate evolutionary biology and ecology at the Paimpont Biological Station (University of Rennes), and her work led to the production of over 170 publications.

In 1963, Annie answered an advertisement for a research candidate to study western lowland gorillas posted by Prof. Pierre-Paul Grassé. She travelled to Gabon in 1964 to study 10 captive gorillas, all of them bushmeat orphans. Dr. Jean-Pierre Gautier joined her in 1965, but when a disease outbreak among the animals forced them to give up this study, they decided to switch focus from the largest of primates to the smallest old-world monkey, the talapoin, and were among the first to study the ecology and social structure of this species.

The Gautiers expanded their study to other cercopithecine species living in the Makokou area of northeastern Gabon, and investigated the complex social relationships observed in polyspecific groups. They discovered how the complementarity of ecological niches and anti-predatory strategies could facilitate inter-species associations. Their research was strengthened through the combination of field observations and captive studies when they established a breeding colony of cercopithecines in Gabon where they could closely observe the animals. In 1969, this breeding centre was transferred to the Biological Station of Paimpont for behavioural studies, and still exists.

After meeting Jonathan Kingdon in 1977, Annie oriented her research towards evolutionary biology. Their collaboration led to the 1988 publication of a benchmark volume "A Primate Radiation: Evolutionary Biology of the African Guenons", co-authored and co-edited by Annie Gautier-Hion, François Bourlière, Jean-Pierre Gautier and Jonathan Kingdon.

In 1989, together with Dr. Marc Colyn, Annie set up a research site in Salonga National Park, Democratic Republic of Congo. Political events brought an end to that project, so Annie established another research station in Gabon, at Makandé. In parallel, she led the ethology research laboratory at the University of Rennes from 1991 to 1999. She also co-authored with Dr. Marc Colyn and Dr. Jean-Pierre Gautier an excellently informative and beautifully illustrated guidebook to central African primates, "Histoire naturelle des primates d'Afrique centrale", published in 1999.

In 1996, Annie finally returned to her initial subject of research, the western lowland gorilla. She set up a research project in Odzala-Kokoua National Park, Republic of the Congo, and launched demographical and behavioral studies in the Maya-Nord and Lokoué clearings. After she retired in 2004, she published a popular book on gorillas, organized multiple public conferences and an exhibition on gorilla conservation.

Annie was an outstanding scientist. We will remember her passion for African forests and their primates, and her dedication to their study and protection. Annie will be greatly missed by all who knew her.

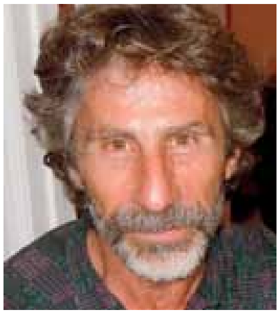
Jean-Pierre Gautier, Damien Caillaud, John Oates, Thomas Struhsaker and Liz Williamson

I worked with Annie Gautier-Hion in Salonga in what is now the Democratic Republic of Congo, and in the Forêt des Abeilles in Gabon, as well as in her research group in France for several years. She was an absolutely great companion in the field and showed me how to see, hear, and understand the monkey species that we studied. I have many fond memories of (mostly hilarious) incidents with her as well as the many astonishing things we saw together in the African rainforest. She was always fascinated by natural history of all kinds, excited to communicate about wildlife, very sympathetic to and respected by, all her African colleagues, from the trackers to the University professors with whom she collaborated. Much of what we know of the ecology of not only the Central African primates, but also many other mammal species, is still based on the work she initiated at the Mpassa research station near Makokou in Gabon in the 1980s.

I last saw her in her cottage in rural Brittany less than a year before she died. Her enthusiasm for life, learning, and living creatures had not diminished. We went for walks in the gorgeous surrounding countryside, and visited the Paimpont research station one last time. Annie was a force of nature and is greatly missed by all who ever spent time in the forests with her, and by her colleagues in centers of learning worldwide.

Fiona Maisels

Alan Richard Mootnick (1951–2011)



White-cheeked gibbon, *Nomascus*. Ricky and Pepper. Photo © Gabi Skollar.

Alan Mootnick, from Los Angeles, California, founded the non-profit "Gibbon Conservation Center" (GCC) in Santa Clarita, California, in 1976. Today it houses the largest collection of endangered apes in the Western Hemisphere. Its mission and his mission: to prevent the extinction of gibbons and to advance the study, propagation, and conservation of the species. Completely self-taught in primatology, he was internationally recognized as a world authority on the taxonomy, biology and captive care of these apes. Alan travelled widely in Asia to share his knowledge, and to train, educate and help local people for the benefit of captive and wild gibbons. He published more than 30 articles in peer-reviewed journals and offered advice to zoos, government agencies, veterinary institutions, and gibbon rescue centers throughout the world. He was the studbook keeper for five species and Husbandry Advisor for the Gibbon Species Survival Plan. A lifetime of extraordinary and brilliant dedication to the conservation and study of gibbons. In the words of his friend and colleague Roland Wirth, Zoological Society for Conservation of Species and Populations (ZGAP), Munich, Germany: "The gibbons lost one of their greatest advocates, the world lost a wonderful person."

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The IUCN/SSC Primate Specialist Group also produces regional newsletters/journals which publish short articles and notes on general and specific aspects of primate ecology, taxonomy, distributions, behavior and conservation, tropical forest ecology and conservation, forest destruction, and protected areas. Also please send information on projects, research groups, events, recent publications, courses, funding sources, activities of primatological societies and NGOs, and other newsworthy items of interest to primate conservationists, directly to the editors at the addresses below.

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Maps should always be made as concise as possible and should include an inset showing the location of the area discussed in relation to its home country or continent.

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We are always interested in receiving high quality photographs for our covers, especially images of little known and rarely photographed primates, even if they do not accompany an article.

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Back cover: Indochinese Silvered Leaf Monkey *Trachypithecus germaini*, in the spirit forest Dong Sakee near the village of Ban Vangsikeo, Dong Phou Vieng National Protected Area, Lao PDR, on 8 April 2012. Photo by Jonathan C. Eames. See page 75.

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