

Primate Diversity and Population Status in the Serranía de San Lucas, Colombia: A Priority Area for Primate Conservation in Northern South America

Andrés Link^{1,2}, Andrés Montes^{1,2}, Juan Carlos Andrade^{2,3}, William Bonell³, Luz Dary Acevedo³
and Ana Gabriela de Luna²

¹*Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia*

²*Fundación Proyecto Primates – Colombia*

³*Wildlife Conservation Society*

Abstract: Although most primates in the Americas are found in Amazonian rainforests and other ecosystems east of the Andean Cordillera, seven platyrrhine genera occur in the inter-Andean valleys, the Caribbean coast and the Pacific lowlands of northwestern South America and Mesoamerica. The Serranía de San Lucas (SSL) is a relatively isolated mountain system at the northern end of the Central Andes of Colombia, and has one of the largest and most undisturbed forests (>2,000,000 ha) of northern South America. Currently, the Serranía de San Lucas is under pervasive, human-induced pressure driven mainly by illegal mining and logging and increasing deforestation for extensive cattle ranching and agriculture. In the last four decades, it has also been largely inaccessible to scientists and conservation initiatives due to political instability. It is home to six primate species, five of them listed as threatened with extinction on the IUCN Red List of Threatened Species: *Ateles hybridus* (Critically Endangered – CR); *Lagothrix lagotricha lugens* (CR); *Cebus versicolor* (Endangered – EN); *Aotus griseimembra* (Vulnerable – VU); *Saguinus leucopus* (VU); and *Alouatta seniculus* (Least Concern – LC). In 2015–2016, we were able to access this region in a joint effort to characterize the biological diversity of the Serranía de San Lucas in collaboration with the local communities. We conducted three short primate surveys: two in the eastern and western lowland forests and one in the montane forests of the Serranía. For the first time in over four decades, we confirmed the presence of all six primates historically occurring in the region. Based on *ad libitum* observations and line-transect censuses, we recorded 128 independent observations of primates. The most relevant findings of these surveys include: (1) location of a population of Colombian woolly monkeys (*Lagothrix lagotricha lugens*) that is isolated from other wild populations of the species; (2) large populations of brown spider monkeys (*Ateles hybridus*) (19.2 ind./km²) and endemic white-footed tamarins (*Saguinus leucopus*) (19.1 ind./km²), (3) the sympatric presence of all six primate genera at the Serranía de San Lucas, and (4) the presence of other ecologically important mammals and birds including lowland tapirs (*Tapirus terrestris*), spectacled bears (*Tremarctos ornatus*) and the Critically Endangered blue-billed curassow (*Crax alberti*). The results from this study highlight the unique opportunity to preserve one of the last of the wild areas in northern South America, thus protecting some of the most endangered primates and the regions wildlife and ecosystems in the intersection of two global Biodiversity Hotspots that provide invaluable services to society at a regional and global scale.

Key words: *Ateles hybridus*, Biodiversity Hotspots, northern Andes, primate conservation

Resumen: En las Américas, la mayor diversidad de especies de primates se encuentra en los bosques amazónicos y en otros ecosistemas al oriente de la Cordillera de Los Andes (ej. Mata Atlántica). Sin embargo, al menos siete géneros de platirrininos tienen una distribución trans-amazónica, la cual incluye los bosques interandinos, las sabanas del norte de Colombia y Venezuela, los bosques del Pacífico y Centroamérica. La Serranía de San Lucas (SSL) es una formación montañosa al norte de la Cordillera Central de Los Andes en Colombia, que contiene uno de los remanentes de bosque más extensos (>2.000.000 ha) y con menor intervención antrópica en el norte de Suramérica. En la actualidad, la SSL tiene unas grandes presiones antrópicas por parte de la minería ilegal y legal y la rápida ampliación de la frontera agrícola y ganadera. Durante las últimas décadas, la SSL ha sido relativamente inaccesible para la comunidad científica debido a la inestabilidad política de esta región. La SSL contiene al menos seis especies de primates (cinco de ellas amenazadas con la extinción): *Ateles hybridus* (CR), *Lagothrix*

lagotricha lugens (CR), *Cebus versicolor* (EN), *Aotus griseimembra* (VU), *Saguinus leucopus* (VU) y *Alouatta seniculus* (LC). Durante 2015 a 2016, tuvimos acceso a la SSL en un esfuerzo con las comunidades locales con el fin de hacer una caracterización biológica de la SSL y resaltar su importancia para la conservación de la biodiversidad. Realizamos tres muestreos, dos en las zonas bajas de la SSL y una en los bosques de montaña de la misma. Por primera vez en al menos cuatro décadas, pudimos confirmar la presencia de las seis especies históricamente distribuidas en esta región de Colombia. A partir de censos en transectos lineales y observaciones oportuniticas obtuvimos 128 registros independientes de primates en la SSL. Los hallazgos más relevantes de estos muestreos incluyen: (1) La confirmación de la presencias de una población de monos churucos (*Lagothrix*) que se encuentra aislada de las demás poblaciones silvestres de este género, (2) Los valores relativamente altos de densidad poblacional de los monos araña café (19.2 ind./km²) y de tití gris (19.1 ind/km²), (3) registros de simpatria entre los tres primates más grandes del norte de Suramérica, (*Ateles*, *Lagothrix* y *Alouatta*), y (4) el registro de otras especies de importancia ecológica como el tapir (*Tapirus terrestris*), el paujil de pico azul (*Crax alberti*) y el oso de anteojos (*Tremarctos ornatus*). Los resultados de estos estudios resaltan la importancia de la SSL para la conservación de la diversidad de primates, mamíferos y en general la diversidad biológica del norte de Suramérica. Así mismo, resalta la inmediata necesidad de proteger la SSL donde confluyen dos Hotspots de biodiversidad global y donde se proveen importantes servicios ambientales a nivel regional y global.

Palabras clave: *Ateles hybridus*, Hotspots de biodiversidad, Andes tropicales, conservación de primates

Introduction

Primates are one of the most diverse groups of placental mammals (apart from rodents and bats) and have colonized most ecosystems in tropical areas and some subtropical regions (Estrada *et al.* 2017). Their relatively slow life history variables and high ecological requirements make them particularly sensitive to population declines and extinction (Jones 2011). More than 60% of the 519 primate species are threatened with extinction, and approximately three out of four species are rapidly declining in numbers (Estrada *et al.* 2017; IUCN 2022). Several synergetic pressures, such as habitat loss, habitat degradation and fragmentation, hunting, pollution and diseases, amongst others, are the main drivers of primate population declines (Estrada *et al.* 2017). Primate habitats largely coincide with areas of high human population growth rates and poverty, and are thus exposed to imminent threats of being unsustainably used to supply urgent, unattended, basic human needs (Potts *et al.* 2010).

Currently, the IUCN has estimated a global diversity of 519 living primate species, with about one-third of them living in Neotropical forests and comprising one of the largest living primate radiations – the platyrrhines (Estrada *et al.* 2017). Although a vast proportion of primate diversity in the Neotropics is concentrated in the Amazon basin, many are also found in two other biogeographic regions: (1) the Atlantic Forest of eastern Brazil, Argentina and Paraguay and, (2) the trans-Andean ecosystems west of the eastern Andes in northwestern South America and Central America.

According to the Asociación Colombiana de Primatología, Colombia is home to at least 38 primate species. The IUCN SSC Primate Specialist Group recognizes 42. There are, however, taxonomic uncertainties that have yet to be resolved, so the exact number is unclear. Colombia is sixth in the ranking of the countries with the highest diversities

of primates, following only Brazil, Madagascar, Indonesia, the Democratic Republic of the Congo (DRC) and Peru. Although most primate species in Colombia are found east of the Andes in the Amazon and Orinoco river basins, a unique set of trans-Andean primates inhabit the lowland valleys between the Northern Andes and along the Pacific and Caribbean lowlands that expand into most of Mesoamerica (Defler 2003). Many of the trans-Andean primates that are found in Colombia are either endemic or restricted to northern South America, and many are categorized as either Critically Endangered or Endangered on the IUCN Red List of the Threatened Species (e.g., *Ateles hybridus*, *Ateles fusciceps*, *Lagothrix lagothricha*, *Saguinus oedipus*, *Saguinus leucopus*, *Cebus versicolor*) (Defler 2003; Mittermeier *et al.* 2013). Northwestern South America has the confluence of two global Biodiversity Hotspots, the Tropical Andes and the Tumbes-Choco-Magdalena (Myers *et al.* 2000). As Biodiversity Hotspots, these regions have a high species richness and large numbers of endemic taxa but also heavily degraded landscapes (Myers *et al.* 2000; Mittermeier and Rylands 2017).

Tropical lowland rainforests, tropical dry forests and wetlands in the inter-Andean valleys (the Río Magdalena and Río Cauca valleys) of northern Colombia have lost more than 80% of their historical forest cover (Etter *et al.* 2006, 2008; Link *et al.* 2013). By 2010, only 22% of the forest of the original distribution of the brown spider monkey (*Ateles hybridus*) remained, and between 1990 and 2010 more than one-fourth of the habitat available in 1990 was transformed into extensive pasture and oil palm plantations (Link *et al.* 2013). A large proportion of these ecosystems have been drastically fragmented (De Luna and Link 2018). Despite the pervasive processes of land transformation and ecosystem degradation, these studies coincide in pointing out the

importance of a handful of remaining biodiversity reservoirs within this unique biogeographical region. The largest continuous forest in the inter-Andean valleys is the Serranía de San Lucas, which is connected to very large tropical lowland forests and seasonally flooded forests in Central Colombia (Fig. 1). There is an urgent need to create protected areas in what can be considered the last remains of the inter-Andean Forest in both the Chocó-Magdalena and Northern Andes Biodiversity Hotspots (Myers *et al.* 2000), as well as to develop community-based conservation initiatives outside of the protected areas (De Luna and Link 2015).

The Serranía de San Lucas holds the highest primate diversity anywhere west of the Andes (trans-Andean distribution) with six species of six different genera (Fig. 2). They include: the brown spider monkeys (*Ateles hybridus*); the Colombian woolly monkey (*Lagothrix lagothricha lugens*); the red howler monkey (*Alouatta seniculus*); the varied white-faced monkey (*Cebus versicolor*); the white-footed tamarin (*Saguinus leucopus*) and the Caribbean or gray-legged night monkey (*Aotus griseimembra*) (Fig. 3).

The presence of Andean night monkeys has still to be confirmed in the highlands of San Lucas.

Earlier studies on primates at the Serranía de San Lucas

Due to the political instability of the past decades in Colombia, several of the most conserved regions in Colombia, including the Serranía de San Lucas, have been inaccessible to science and conservation (Fjeldsa *et al.* 2005; Davalos 2001). Many scientists, including some of the most experienced primatologists in Colombia, have identified the Serranía de San Lucas as one of the priority areas for the conservation of biological diversity in northern South America (Defler *et al.* 2003; Defler 2013). It may well be the last wildlife refuge in the inter-Andean ecosystems and the lower and middle Río Magdalena basin, unequivocally the area with highest forest cover and connectivity in the region (Link *et al.* 2013). The Serranía de San Lucas has a unique biodiversity and has been identified as a priority area for the conservation of birds and mammals in Colombia, especially as there are no protected areas there, and mining and agriculture continue to increase (Alvarez 2002; Defler *et al.* 2003).

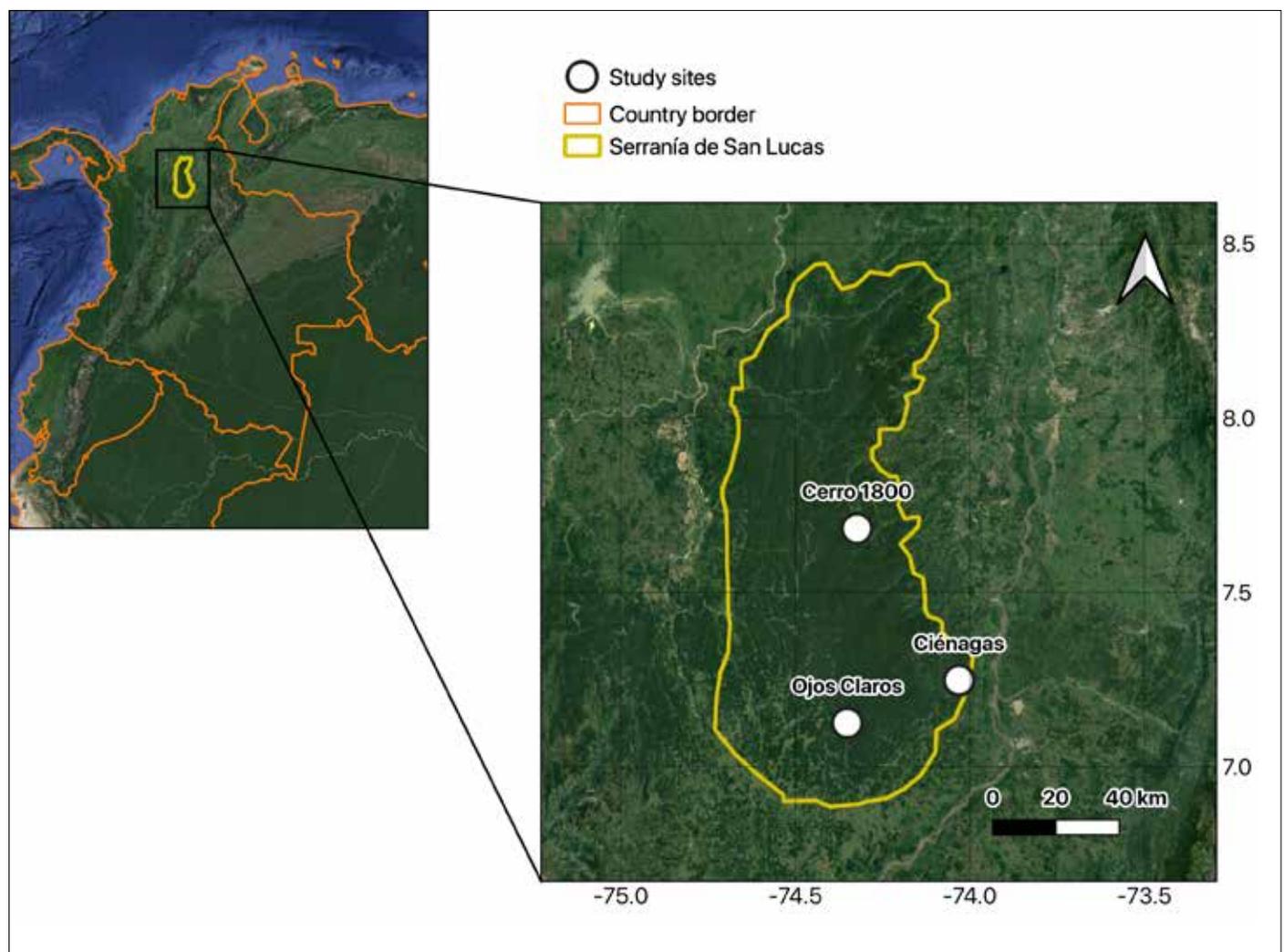


Figure 1. The location of the Serranía de San Lucas, Colombia.

Field studies and biological surveys at San Lucas are scant and mostly limited to studies in the early and mid 1900s. Prior to our expedition, the last biological collections of birds there was in the 1940s (de Schauensee 1948) and covered only the lowlands surrounding the montane forest. Some short surveys have provided further notes on avian diversity and distribution in this isolated mountain range (Salaman *et al.* 2002; Donegan 2012). The conservation value of the Serranía de San Lucas has been recognized due to the presumed presence of an ample biodiversity and indirectly because of the immense forest cover (>2.000.000 ha) in between one of the most pervasively transformed regions in South America.

Some of the earliest studies on wild primate populations at San Lucas date to the mid-70s. There, Kavanagh and Dresdale (1975) conducted one of first descriptions of the behavior of woolly monkeys in their natural environment. Over two months, Kavanagh and Dresdale (1975) collected behavioral data on two groups which led them to conclude that these large primates lived in large groups of up to 18 individuals and were almost exclusively found in mature forest. Bernstein *et al.* (1976) conducted the first evaluation of the

primate populations in the northern region of the Serranía in both continuous and fragmented forests. They recorded all five diurnal primates in the region and mentioned the existence of night monkeys (*Aotus griseimembra*). In areas with minimal human intervention, large ateline primates (*Ateles* and *Lagothrix*) were generally the most common (Bernstein *et al.* 1976). Bernstein *et al.* (1976) estimated the population density of spider monkeys and woolly monkeys at 9 and 14 ind./km², respectively, and concluded that the large atelines were extremely vulnerable to habitat degradation and hunting. In fact, populations of woolly monkeys were extirpated from small forest fragments, while brown spider monkeys were close to extinction (Bernstein *et al.* 1976). Finally, the third and last study of primates of the Serranía de San Lucas also aimed to estimate primate population densities in a relatively small forest fragment (83 ha) in the north of the range (Green 1978). Green showed that brown spider monkeys and red howler monkeys were the most abundant (33 ind./km² and 22 ind./km², respectively). Thirty-five years after these initial surveys, Roncancio *et al.* (2013) censused the northern part of Serranía and found relatively large populations of brown spider monkeys (32 ind./km²) and the

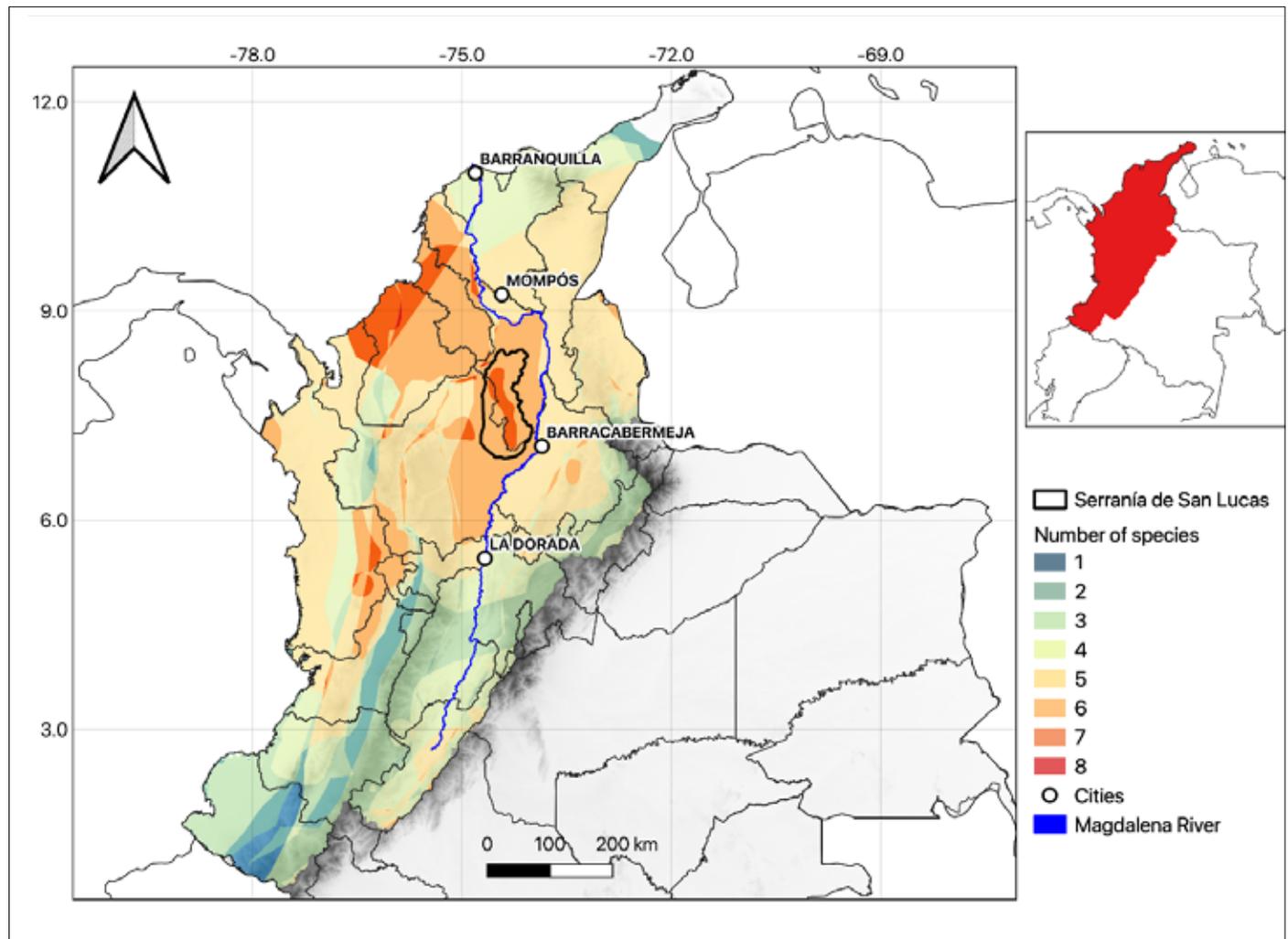


Figure 2. Primate species richness in the Cauca-Magdalena interfluvium in northern South America.

other sympatric primates except the woolly monkeys were observed in the study area.

The Serranía de San Lucas is a priority area for wildlife conservation in northern Colombia, vital for the protection of viable populations of its six primates and one of the most unique biogeographic regions in northern South America. The conservation of the Serranía should be implemented

immediately as it (1) is the largest continuous forest in the inter-Andean valleys, (2) has the highest primate diversity of trans-Andean ecosystems, and (3) is the only region where two of the largest platyrrhines of Colombia (*Ateles* and *Lagothrix*) live in sympatry. Here, we present recent data on the occurrence and population status of primates there during three short surveys in 2015 and 2016. The surveys were carried out in extremely short windows of time when

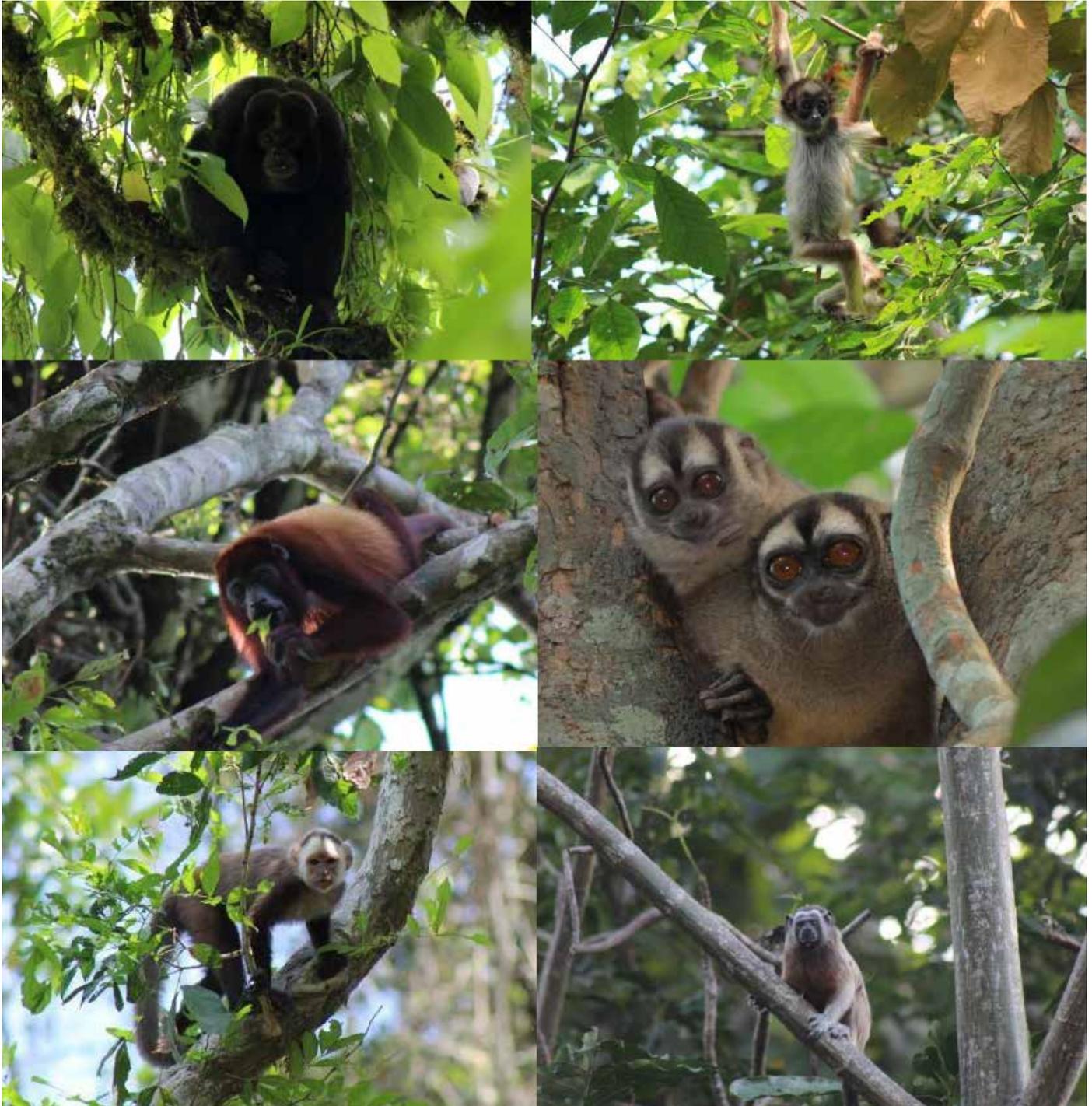


Figure 3. Primates of the Serranía de San Lucas. **Left column** from top to bottom: the Colombian woolly monkey (*Lagothrix lagothricha lugens*), the red howler monkey (*Alouatta seniculus*) and the varied white-fronted capuchin (*Cebus versicolor*). **Right column** from top to bottom: the brown spider monkey (*Ateles hybridus*), the Caribbean or gray-legged night monkey (*Aotus griseimembra*) and the white-footed tamarin (*Saguinus leucopus*). Photographs by Andrés Link.

we were able to participate in a community-based biodiversity study with the main goal of supporting the urgent need to protect the remaining forests and wetlands.

Methods

From 2015–2016, we visited three different sites in the Serranía de San Lucas and conducted preliminary primate surveys, a component of a broader project to study the biodiversity of the region in order to prioritize conservation actions in Central Colombia. Surveys were coordinated with local communities, FUNCOPROMAS and the Asociación Campesina del Valle del Río Cimitarra (ACVC). They organized the logistics of each field session and co-developed research activities. We first conducted a primate census at Ojos Claros (7°7'30.72"N, 74°21'3.24"W) in the southwestern part of the Serranía from 12 April to 11 May 2015 (30 days) in an area with little human intervention. Second, we were able to participate in a 5-day visit to Cerro 1800 (7°40'58.44"N, 74°19'22.44"W) during July 2015, in the Central highlands of the Serranía. We conducted the third primate survey at Ciénagas (7°14'52.44"N, 74°1'49.80"W) in the lowland wetlands of the southeastern region of the Serranía in October 2016 (Fig. 1).

On all surveys, we walked through the trails at an average speed of 1 km/h following the recommendations for line transect censuses described by Peres (1999), stopping every 200 m for a period of two minutes in order to increase our chances of detecting primates and other wildlife. For each observation of a primate group or individuals, we recorded their location with a GPS, the species observed and recorded group size and age-sex categories, whenever possible. We also recorded the perpendicular distance of the animal to the trail. All transects were sampled during daylight hours, and information on the presence of the only nocturnal primate (*Aotus griseimembra*) was collected opportunistically when we found nesting sites or when they were observed by other team members during night surveys of other taxa (e.g., amphibians).

We estimated primate population densities for each of the diurnal primate species observed during line transect surveys. We used King's method (Leopold 1933), and Distance sampling (Thomas *et al.* 2010). For King's method, we used the following formula: $D = n/L(2a)$, where D represents the density of groups or individuals per area, n is the number of groups or individuals observed during surveys, L is the total length walked during the entire survey and a represents average transect width estimated from all perpendicular distances for each species, separately. Group size was estimated based on the average value of the number of individuals observed across the study, for each primate taxon separately. Distance sampling methods were only used to calculate primate densities at Ojos Claros for those primate species that had more than 20 independent observations. We used the perpendicular distance model that best fitted the distribution of data based on the following five

models: (1) default half-normal key with cosine polynomial expansion, (2) uniform key with cosine polynomial expansion, (3) uniform key with simple polynomial expansion, (4) half-normal key with hermite polynomial expansion, and (5) hazard-rate key with the cosine polynomial expansion. Based on Buckland *et al.* (2001), we selected the model with the lowest Akaike (AIC) value. Group size was estimated using a "Cluster-size biased regression" unless the software recommended the use of average group size. We truncated 5% of extreme data to reduce the effect of outlier data on our analyses.

Survey I: Vereda Ojos Claros, Remedios, Antioquia (Ojos Claros)

At Ojos Claros, we were able to intensively survey nine line transects (1.2–8.7 km) during a period of 22 sampling days. Surveys were done independently by two teams, each comprised a local guide and one of our field biologists. Overall, transects were surveyed from 1 to 7 times, accounting for a total sampling effort of 90.1 km.

Survey II: Vereda de San Juan, Santa Rosa, Bolívar

Surveys were carried out during a 5-day biodiversity assessment (24–29 July 2015) conducted with the local communities of FUNCOPROMAS, so as to characterize the diversity of main biological groups (e.g., terrestrial vertebrates, insects, plants, amongst others). We set three "line" transects at Cerro 1800 along existing trails aiming to cover a broad altitudinal range (580–2000 m) in the montane forests of the Serranía de San Lucas. All transects were at least 1-km long and were independent of each other. We surveyed approximately 15 km of transects during this short survey. Other members of the biological expedition recorded *ad libitum* observations of primates during surveys on other biological groups.

Survey III: Ciénaga de San Lorenzo, Bolívar

"Ciénagas" is located in the forests and wetlands on the south-eastern lowlands of the Serranía de San Lucas. The broader region comprises the lower Río Cimitarra basin and the seasonally flooded plains of the Río Magdalena, in the municipalities of Cantagallo and Yondo. Surveys were carried out in four locations: (1) Bajo la Manigüa, 7°05'07.02"N, 74°10'05.61"W, (2) La Poza, 7°08'07.45"N, 74°05'32.88"W, (3) Sábalo Viejo, 7°10'17.17"N, 74°01'41.12"W, and (4) Ciénaga de San Lorenzo/Yanacue, 7°17'47.32"N, 74°01'29.41"W. Line transect surveys were conducted during the rainy season in October 2016, which made field work challenging due to large areas that are seasonally flooded. We thus conducted censuses on pre-existing trails in forests and wetlands in the area. We walked 11 transects in the four areas that included relatively undisturbed forests as well as fragments within a matrix of cattle pastures and some small-scale mining.

Results

We confirmed the presence of six primates during the three primate surveys conducted in the central and southern areas of the Serranía de San Lucas. We recorded three species (*L. lagotrucha*, *A. hybridus* and *S. leucopus*) during line transect surveys in the montane forests of Cerro 1800 (Table 1), and other members of the biological survey confirmed the presence of the other three primate species (*A. seniculus*, *C. versicolor* and *A. griseimembra*) through direct observations while working with local assistants.

At Ciénagas, we completed a total of 96.3 km of surveys and recorded all five species in the lowland forests of the Serranía. Overall, we made 55 independent observations during the surveys: *A. hybridus* (n = 7), *A. seniculus* (n = 13), *C. versicolor* (n = 6), *S. leucopus* (n = 24) and *A. griseimembra* (n = 5) (Table 1). Other landscape species such as jaguar (*Panthera onca*) and lowland tapirs (*Tapirus terrestris*) were recorded by their tracks.

At Ojos Claros we surveyed 90.1 km and recorded all five primate species present in the lowland forests of the Serranía de San Lucas. We obtained 64 independent observations of primates, half of them were of the brown spider monkey (*A. hybridus*). White-footed tamaris were also common (n = 21 observations), howler monkeys were observed six times and white fronted capuchins only twice (Table 2). Caribbean night monkeys (*A. griseimembra*) were also sighted several times in *ad libitum* sampling and by many members of the team, who were surveying for amphibians and reptiles at night. We also saw spectacled bears (*Tremarctos ornatus*) and crested eagles (*Spizaetus ornatus*) during line-transect surveys. The Critically Endangered blue-billed curassow (*Crax alberti*) was also seen during these surveys, and its

presence further supports the urgent need for effective conservation strategies at the Serranía de San Lucas.

We estimated population densities for four diurnal species at Ojos Claros using King's method. We used Distance sampling only for *A. hybridus* and *S. leucopus* (Table 2). Both *A. hybridus* and *S. leucopus* were common there and population estimates were similar at approximately 19 ind./km² (Table 2). Brown spider monkeys were observed in subgroups, solitary individuals, and in larger groups of up to 21 individuals. Most subgroups of spider monkeys were composed of three to four individuals, just a few were relatively large (>10 individuals) (Fig. 4). Group size in *S. leucopus* ranged from 2 to 9 individuals, while sightings of red howler monkeys and white-faced capuchins were too few to make any meaningful indication of their grouping patterns (Fig. 4).

Discussion

The results from primate surveys in the lowland and montane forests of the Serranía de San Lucas highlight the importance of this large biogeographical region for the conservation of extant platyrrhines and the diverse biological communities of northern South America. We confirmed the presence of at least six primates (*Ateles hybridus*, *Lagothrix lagotrucha*, *Alouatta seniculus*, *Saguinus leucopus*, *Cebus versicolor* and *Aotus griseimembra*) confirming that this region has the highest primate species richness west of the Eastern Andes. All primate genera with a trans-Andean distribution are present at the Serranía de San Lucas except for the squirrel monkey (*Saimiri*) (Defler 2003).

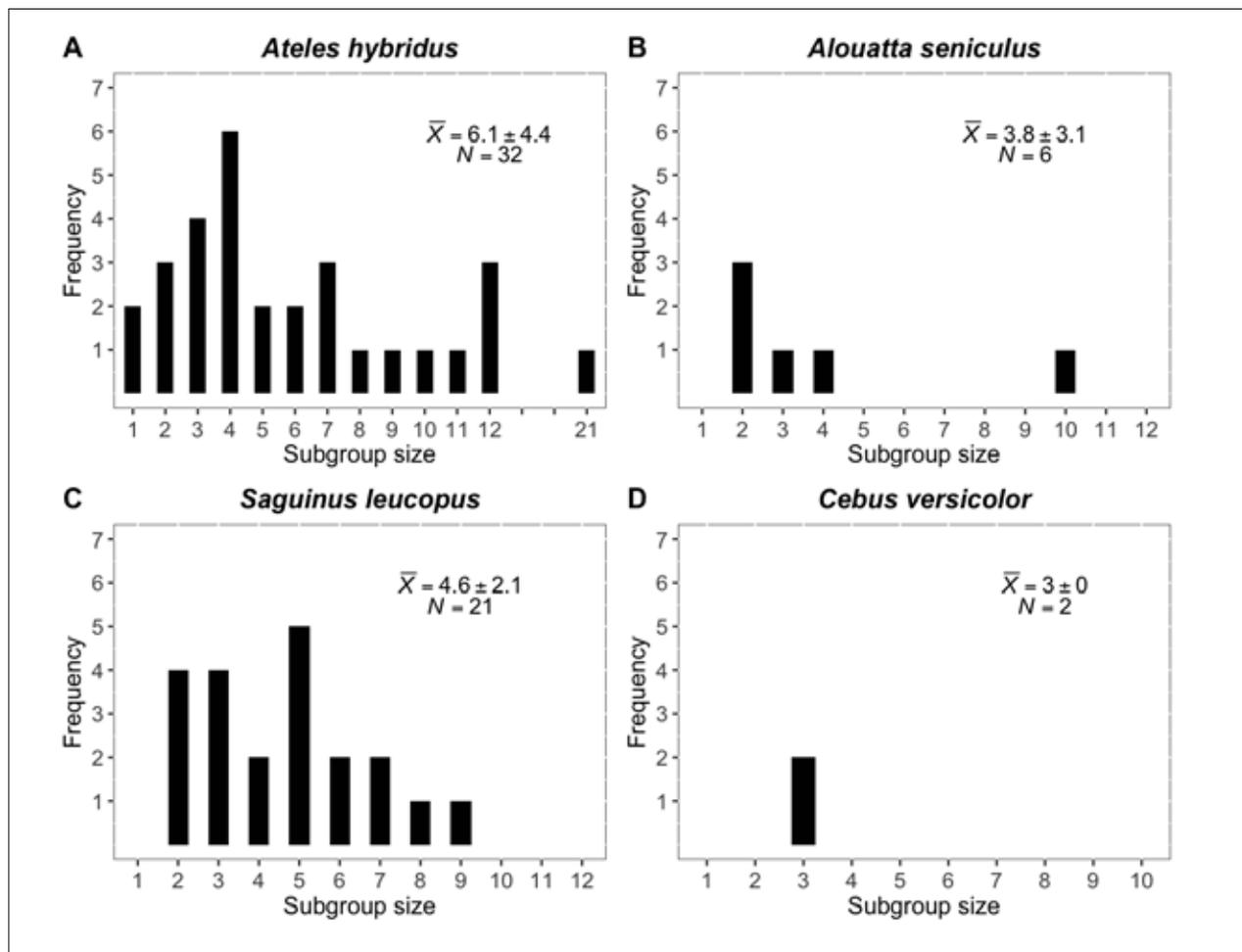
The population of Colombian woolly monkeys (*Lagothrix lagotrucha lugens*) in the montane forests had not been

Table 1. Sampling effort and primate records at the Serranía de San Lucas. Asterisks refer to *ad libitum* observations of primate species by other team members.

Area	Site	Coordinates	Altitude (m)	Sampling effort (km)	<i>A. hybridus</i>	<i>L. lagotrucha</i>	<i>A. seniculus</i>	<i>C. versicolor</i>	<i>S. leucopus</i>	<i>A. griseimembra</i>
Cerro 1800			950–1530	~15	2	4	*	*	3	*
Ciénagas	La Manigua	7°05'07.0"N 74°10'06.5"W	80	38.6	5		3	3	3	1
	La Poza	7°08'07.4"N 74°05'32.8"W	80	14.2	1		3	1	7	1
	Sábalo Viejo	7°10'17.1"N 74°01'41.1"W	70	10.5			6		1	
	San Lorenzo/ Yanacué	7°17'47.3"N 74°01'29.1"W	70–220	35.2	1		1	2	13	3
	Total		70–220	98.5	7		13	6	24	5
Ojos Claros	Total			90.1	32		6	2	21	*

Table 2. Primate population densities at Ojos Claros, Serranía de San Lucas.

Species	Presence	Records	Groups/km ²		Ind./km ²	
			King	Distance	King	Distance
<i>A. hybridus</i>	Yes	32	8.7	3.1 (2.0-4.8)	54.3	19.2 (11.6-31.7)
<i>S. leucopus</i>	Yes	21	9.4	4.4 (2.5-7.6)	42.9	19.1 (10.6-34.6)
<i>C. versicolor</i>	Yes	2	0.6	-	1.9	-
<i>A. seniculus</i>	Yes	5	2.0	-	8.2	-
<i>A. griseimembra</i>	Yes	1	-	-	-	-
<i>L. l. lugens</i>	No	0	-	-	-	-

**Figure 4.** Group sizes for four sympatric primate species at Ojos Claros estimated through line transect surveys. Note that data for *A. hybridus* corresponds to subgroups given their high-degree of fission-fusion dynamics.

recorded (amongst the scientific community) for over four decades (see Defler 1996). The Colombian endemics *A. hybridus* and *S. leucopus* were found in relatively high population densities, and the conservation of the Serranía de San Lucas should be a national and regional priority to protect its six primates, five of them threatened with extinction, and the megadiverse ecosystem it represents (Hernandez-Camacho and Defler 1989; Defler 2013).

Estimated population densities for the Critically Endangered *A. hybridus* at Ojos Claros fall within values obtained in other studies in fragmented and continuous forests (De Luna and Link 2018) but are lower than those reported by Roncancio *et al.* (2013) in the northern region of the Serranía (see methodological considerations below). High primate population densities in “young” forest fragments have been largely associated with the early effects of fragmentation,

where primates are restricted to smaller areas and exposed to higher levels of intra- and inter-specific competition (Link *et al.* 2010). In contrast, population densities of *A. seniculus* and *C. versicolor* at the Serranía de San Lucas were relatively low, which is often common at Amazonian sites with minor interventions (Derby 2008) but contrast, for example, with studies in fragmented landscapes (in riparian forests) of the Rio Magdalena basin (Bernstein *et al.* 1976; Link *et al.* 2010).

This study provides the most recent data on the coexistence of a diverse primate community in some of the last remaining forests of northern South America. Although the population density estimates at Ojos Claros seem quite high when compared to other primate population estimates in the region (see De Luna and Link 2018), it is important to acknowledge that the methodological design implemented in these surveys violates several assumptions of line-transect censuses and Distance sampling analyses (Thomas *et al.* 2010). Although we estimated population densities for *A. hybridus* and *S. leucopus* at Ojos Claros as they had the largest number of independent detections (32 and 21, respectively), these sample sizes might still be too small to provide reliable estimates. Also, the number of transects surveyed in each study area was small, and most of them were not set randomly in the landscape but rather followed paths used by local communities. For the data presented here, it is important to note that population density is determined by the carrying capacity, being a dynamic parameter that varies in time and space; it is, therefore, important to bear in mind that an assessment derived from a few places at a specific point in time cannot be conclusive about regional population trends (Coulson *et al.* 2001; Rudran and Fernández-Duque 2003).

The Serranía de San Lucas is without doubt the largest continuous forest of the inter-Andean ecosystems (>2,000,000 ha), and comprises a large ecosystem diversity that includes wetlands, lowland rainforests, tropical dry forests and submontane and montane forests. The Serranía has one of the most intact biological communities in northern South America, highlighting its irreplaceability and immense conservation value. Most primatological studies in the Río Magdalena valley and northern Colombia have taken place in fragmented and degraded habitats (Link *et al.* 2010; De Luna and Link 2018). Most probably these populations are exposed to novel human-induced impacts on their habitats and populations, and thus may be ecologically and behaviorally attempting to adapt to this rapidly changing environment. Studies in undisturbed regions, such as the Serranía de San Lucas can offer the opportunity to better understand how primate communities are structured, as well as how they evolved to cope with living in the complex tropical inter-Andean forests. Relevant at the regional level, for primates and other important species such as the jaguar, the lowland tapir, and the blue-billed curassow, is that the quality and size of these relatively intact ecosystems means that they act as a source that contributes to the regulation of wildlife abundance in nearby smaller and frequently

degraded forests (Pulliam 1988). The fragments around the Serranía vary in size and structure. They are much smaller, and much of the region of the Magdalena Medio could be considered a sink, unable to support viable populations (Días 1996). The source-sink models explain that given the good conditions of the sources, the populations of different species could increase. An excess of individuals would allow some to move to the sinks, and in this way populations could be maintained in places with lower quality habitat (Johnson 2004). As such, the populations of the sources could be important for the long-term survival of a large population.

The frequent encounters with wild primate groups and the high population-density estimates of *A. hybridus* and *S. leucopus* in the undisturbed forests of Ojos Claros, provide strong evidence of the importance of the Serranía de San Lucas to protect some of the last viable populations of threatened and endemic primates in northern Colombia. The isolated population of *L. lagothericha* in the montane forests of the Serranía, for example, should be considered a Conservation Unit in itself as it is isolated from the Amazonian populations, and those still present in the Eastern Andes in Colombia (e.g., Medina, Bosques de Galilea, Cueva de Los Guacharos and Alto Fragua Indi Wasi national parks) (Vargas *et al.* 2014).

Noteworthy is that the coexistence of sympatric populations of wild spider monkeys and woolly monkeys has been largely attributed to habitats with high fruit productivity, providing sufficient resources for two of the largest arboreal frugivores in the Americas to coexist. In Amazonian forests, these two atelins are most often found in sympatry in western Amazonian forests with high productivity (e.g., Tinigua National Park, Colombia; Yasuni National Park, Ecuador). The presence of *Ateles* and *Lagothrix* is indicative of its productivity and ecological heterogeneity, and its potential to hold a unique and megadiverse wildlife community.

The existence of populations of the largest primates also suggests that some of the key processes for forest maintenance, through seed dispersal services, are still in place (Link and Di Fiore 2006) and probably maintaining other important ecosystem services such as carbon sequestration (Peres *et al.* 2016). Reducing or losing primate populations through hunting and habitat loss and degradation may well foster additional negative impacts on local forest dynamics and the services they provide at both local and global scales.

We emphasize that the Serranía de San Lucas is probably one of the most important areas for the conservation of biodiversity and ecosystem services in northern South America. While numerous species remain to be discovered within its poorly studied ecosystems, the current threats to one of the last reservoirs of biodiversity in northern Colombia are increasing at accelerated rates. Legal and illegal gold mining, selective logging for hardwoods, illegal crops and pervasive deforestation for large-scale cattle ranching and agroindustry are imminent threats. Immediate action is needed to reconcile the conservation of biological systems with local sustainable livelihoods in order to guarantee the

protection of one of the last continuous forests in northern Colombia.

The Serranía de San Lucas is probably one of the last remaining continuous forests containing viable populations of Critically Endangered primates such as *Ateles hybridus* and other wildlife that require large areas. National and regional protected areas are urgently needed, integrating them with complementary conservation strategies outside protected areas (De Luna and Link 2015) in order to protect, jointly with local communities and other stakeholders, one of the most important wildlife hotspots in the Americas.

Acknowledgments

We thank the local communities at Serranía de San Lucas and in particular FUNCOPROMAS and the Asociación Campesina del Valle del Río Cimitarra (ACVC) for coordinating the logistics to conduct this study. We also thank Parques Nacionales Naturales de Colombia, Fundación Santo Domingo, Grupo Argos, the Conservation Leadership Program, the Margot Marsh Biodiversity Foundation's Primate Action Fund administered by Re:wild, and the Mohamed bin Zayed Species Conservation Fund for financial support. Fundación Proyecto Primates and WCS-Colombia also provided logistic support and coordinated permits and administrative processes associated with this study. We are also most grateful to Thomas R. Defler and an anonymous reviewer for their valuable comments and suggestions concerning this article. Finally, we thank Anthony Rylands for the thorough editorial revision of this article.

Literature Cited

- Alvarez, M. D. 2002. Illicit crops and bird conservation priorities in Colombia. *Conserv. Biol.* 16: 1086–1096.
- Bernstein, I. S., P. Balcaen, L. Dresdale, H. Gouzoules, M. Kavanagh, T. Patterson and P. Neyman-Warner. 1976. Differential effects of forest degradation on primate populations. *Primates* 17: 401–411.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to Distance Sampling*. Oxford University Press, Oxford.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay Sheep. *Science* 292: 1528–1531.
- Dávalos, L. M. 2001. The San Lucas mountain range in Colombia: how much conservation is owed to the violence? *Biodiv. Conserv.* 10: 69–78.
- Defler, T. R. 1996. The IUCN conservation status of *Lagothrix lagothricha lugens* Elliot, 1907. *Neotrop. Primates* 4: 78–80.
- Defler, T. R. 2003. *Primates de Colombia*. Conservación Internacional Colombia, Bogotá, D.C.
- Defler, T. R., J. V. Rodríguez-Mahecha and J. I. Hernández-Camacho. 2003. Conservation priorities for Colombian primates. *Primate Conserv.* (19): 10–18.
- Defler, T. R. (2013). Aspectos sobre la conservación de los primates colombianos: ¿Cuál es el futuro? In: *Primates Colombianos en Peligro de Extinción*, T. R. Defler, P. R. Stevenson, M. L. Bueno and D. C. Guzmán-Caro (eds.), pp. 3–22. Asociación Primatológica Colombiana, Bogotá, D.C.
- De Luna, A. G. and A. Link. 2015. Conservación del mono araña café (*Ateles hybridus*) y otros primates fuera de áreas protegidas en Colombia. In: *Conservación de Grandes Vertebrados en Áreas no Protegidas de Colombia, Brasil y Venezuela*, E. P. Garrido, C. A. Lasso and C. Castaño-Urbe (eds.), pp. 275–293. Serie Fauna Silvestre Neotropical Tropical Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, D.C.
- De Luna, A. G., Y. García-Morera and A. Link. 2016. Behavior and ecology of the white-footed tamarin (*Saguinus leucopus*) in a fragmented landscape of Colombia: small-bodied primates and seed dispersal in Neotropical forests. *Trop. Conserv. Sci.* 9: 788–808.
- De Luna, A. G. and A. Link. (2018). Distribution, population density and conservation of the Critically Endangered brown spider monkey (*Ateles hybridus*) and other primates of the inter-Andean forests of Colombia. *Biodiv. Conserv.* 27: 3469–3511.
- Derby, A. M. 2008. Investigating How Ecology and Demography Influence Folivorous Primate Biomass in the Western Amazon. PhD thesis, State University of New York at Stony Brook, NY.
- De Schauensee, R. M. 1948. The birds of the Republic of Colombia: their distribution, and keys for their identification. *Caldasia* 5: 251–379.
- Días, P. C. 1996. Sources and sinks in population biology. *Trends Ecol. Evol.* 11: 326–330.
- Donegan, T. M. 2012. Range extensions and other notes on the birds and conservation of the Serranía de San Lucas, an isolated mountain range in northern Colombia. *Bull. Brit. Ornithol. Club* 32: 140–161.
- Estrada, A. 2017. Impending extinction crisis of the world's primates: why primates matter. *Sci. Adv.* 3: e1600946.
- Etter, A., C. McAlpine, K. Wilson, S. Phinn and H. Possingham. 2006. Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, Ecosyst. Environ.* 114: 369–386.
- Etter, A., C. McAlpine and H. Possingham. 2008. Historical patterns and drivers of landscape change in Colombia since 1500: a regionalized spatial approach. *Ann. Assoc. Am. Geogr.* 98: 2–23.
- Fjeldså, J., M. D. Alvarez, J. M. Lazcano and B. Leon. 2005. Illicit crops and armed conflict as constraints on biodiversity conservation in the Andes region. *Ambio* 34: 205–211.

- Green, K. M. 1978. Primate census in northern Colombia: a comparison of two techniques. *Primates* 19: 537–550.
- Hernández-Camacho, J. and T. R. Defler, 1989. Algunos aspectos de la conservación de primates no-humanos en Colombia. In: *Anales del Simposio de Primatología del IX Congreso Latinoamericano de Zoología, Arequipa, Perú, 9–15 Octubre, 1983*, C. J. Saavedra, R. A. Mittermeier and I. B. Santos (eds.), pp. 67–100. WWF-US, Washington, DC.
- IUCN. 2022. The IUCN Red List of Threatened Species. International Union for Conservation of Nature (IUCN), Cambridge, UK, and Gland, Switzerland. <<https://www.iucnredlist.org/>>.
- Jones, J. H. 2011. Primates and the evolution of long, slow life histories. *Curr. Biol.* 21: 708–717.
- Johnson, D. M. 2004. Source-sink dynamics in a temporally, heterogeneous environment. *Ecology* 85: 2037–2045.
- Kavanagh, M. and L. Dresdale. 1975. Observations on the woolly monkey (*Lagothrix lagothricha*) in northern Colombia. *Primates* 16: 285–294.
- Leopold, A. 1933. *Game Management*. Charles Scribner's Sons, New York.
- Link, A. and A. Di Fiore. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *J. Trop. Ecol.* 22: 235–246.
- Link, A., A. G. De Luna, F. Alfonso, P. Giraldo-Beltran, and F. Ramirez. 2010. Initial effects of fragmentation on the density of three Neotropical primate species in two lowland forests of Colombia. *Endang. Species Res.* 13: 41–50.
- Link, A., A. G. De Luna and J. Burbano. 2013. Estado de conservación de uno de los primates más amenazados con la extinción: el mono araña café (*Ateles hybridus*). In: *Primates Colombianos en Peligro de Extinción*, T. R. Defler, P. R. Stevenson, M. L. Bueno and D. Guzman, (eds.), pp. 87–117. Asociación Primatológica Colombiana, Bogotá, DC.
- Mittermeier, R. A. and A. B. Rylands. 2017. Biodiversity Hotspots. In: *Encyclopedia of the Anthropocene. Volume 3: Biodiversity*, T. E. Lacher Jr. (ed.), pp.67–75. Elsevier Inc., New York.
- Mittermeier, R. A., A. B. Rylands and D. E. Wilson (eds.). 2013. *Handbook of the Mammals of the World, Volume 3, Primates*. Lynx Edicions. Barcelona.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature, Lond.* 403: 853–858.
- Peres, C. A. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. *Neotrop. Primates* 7: 11–16.
- Peres, C. A., T. Emilio, J. Schiatti, S. J. Desmoulière and T. Levi. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci.* 113: 892–897.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25: 345–353.
- Pulliam, D. W. 1988. Sources, sinks, and population regulation. *Am. Nat.* 135: 652–661.
- Roncancio N. J., K. Gomez and F. Quintero-Sandoval. 2013. Comparisons of populations density and group structure for the variegated spider monkey (*Ateles hybridus*), Serranía de San Lucas (Bolívar). In: *Primates de Colombia en Peligro de Extinción*, T. R. Defler and P. R. Stevenson (eds.), pp. 235–248. Asociación Primatológica Colombiana, Bogotá, D.F.
- Rudran, R. and E. Fernández-Duque. 2003. Demographic changes over thirty years in a red howler population in Venezuela. *Int. J. Primatol.* 24: 925–947.
- Salaman, P., T. M. Donegan and A. M. Cuervo. 2002. New distributional bird records from Serranía de San Lucas and adjacent Central Cordillera of Colombia. *Bull. Brit. Ornithol. Club* 122: 285–303.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47: 5–14.
- Vargas, S. A., J. Leon, M. Ramirez, N. Gakvis, E. Cifuentes and P. R. Stevenson. 2014. Population density and ecological traits of highland woolly monkeys at Cueva de los Guacharos National Park, Colombia. In: *High Altitude Primates*, N. B. Grow, S. Gursky-Doyen and A. Krzton (eds.), pp. 85–102. Springer, New York.

Corresponding author: Andrés Link
E-mail: <a.link74@uniandes.edu.co>

Received for publication: 30 April 2022

Revised: 2 July 2022