Developments in Primatology: Progress and Prospects
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Thomas R. Defler
Pablo R. Stevenson *Editors*

The Woolly Monkey

Behavior, Ecology, Systematics, and Captive Research

Springer

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Contents

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Part I
Introduction

Chapter 1
Introduction: Studying Woolly Monkeys

Thomas R. Defler and Pablo R. Stevenson

Abstract Woolly monkeys are large Neotropical primates widely distributed in most of the Amazon basin and in the Northern Andes, living in forests from see level up to 2,500 m. Two species have been recognized since the first taxonomic revision (one small population in the Peruvian Andes and a widespread one in the rest of the range), and current evidence supports this view. Woollies live in relatively large groups with multiple males and multiple females and their offspring. Females migrate from their natal groups more often than males and males are tolerant with other males and aggressive toward females. Estrous females commonly copulate with all adult males in the group, and infanticide has not been reported in natural populations. Group cohesion varies and in some populations woolly monkeys show fluid fission-fusion groupings. Woolly monkeys prefer ripe fruit and complement their diet with young leaves, arthropods, small vertebrates, unripe fruits and flowers. This primate has a long history of interaction with humans, particularly because they are preferred hunting targets of indigenous people across their geographical range. Woolly monkeys are hunted for nutritional reasons, but in some cases they have been captured as bait for hunting spotted cats, as pets, and for biomedical purposes. Because of hunting and habitat loss, natural populations have declined and they have been eliminated from many regions within their original distribution. Captive colonies are common, but reproduction and survival in captive conditions occur at low rates. The subspecies living in the Andean region have suffered the most and are now considered Critically Endangered (CR) by IUCN standards. In this chapter, we relate the history of research on these primates and we briefly describe the contents of this book.

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Woolly monkeys are some of the largest neotropical primates along with the rest of the atelids, including muriqui, spider monkeys, and howler monkeys. As such, they have a large impact on tropical forests; they usually attain a high biomass where they are found and they exercise a strong influence on forest diversity, since they disperse hundreds of forest trees, insuring that tree species are widely found throughout these monkeys' habitat (Stevenson 2000, 2002, 2004a; Laverde et al. 2002; Stevenson and Garcia 2003; Stevenson et al. 1997a, 2002, 2005; Gonzalez and Stevenson this volume). Serious study of woolly monkeys in their natural habitat began only a few years back and primarily took place in Colombia (Nishimura and Izawa 1975; Izawa 1975, 1976; and especially Nishimura 1988, 1990a, b, 1994, 1997, 1999a, b, 2003; Nishimura et al. 1992, 1995; Sakurai and Nishimura 2000; and Yumoto et al. 1999). Lately, a very large effort has been sustained by one of us (P. Stevenson) studying *Lagothrix lagothricha lugens* in the western Colombian Amazon, to clarify some of the important aspects of woolly monkeys and this effort continues as one of the most intense concentrations on a neotropical species to date, first on the Río Duda and the Tinigua National Park (Stevenson 1992, 1997a, b, 1998, 1999, 2000, 2003, 2004a, b, 2006, 2007, 2011; Stevenson and Castellanos 2000; Castellanos et al. 1999;Stevenson and Quiñones 1993, 2004; Stevenson and Medina 2003; Stevenson and Aldana 2008; Stevenson and Garcia 2003; Stevenson and Guzman 2010; Gonzalez and Stevenson 2010; and Stevenson et al. 1994, 1997b, 1998, 1999, 2000, 2005a, b). A more modest effort has been carried out by the other editor at a different site and with the second taxon (*L. l. lagothricha* Defler 1987, 1995, 1996a, b, 1999, 2013, this volume; Defler and Defler 1996) on the Apaporis River in the eastern Colombian Amazon. Recent studies on this biological station (Caparu) were undertaken by Gonzalez and Stevenson (2009, 2010). Other earlier studies had taken place particularly in Peru by Soini (1986, 1990) and in Brazil by Peres (1991, 1994, 1996). Additionally, we note a new focus of *Lagothrix* studies developing in Ecuador in Yasuni National Park (Di Fiore 1997, 2003, 2004; Di Fiore and Rodman 2001; Di Fiore and Fleischer 2004, 2005; Di Fiore et al. 2006, 2009; Di Fiore and Suarez 2007; and Dew 2005) and Brazil (Iwanaga and Ferrari 2001). The literature on *L. flavicauda* has been less extensive; however, the information is starting to accumulate (e.g., Mittermeier et al. 1975; Leo Luna 1980, 1982, 1987, 1989; DeLuycker 2007; Cornejo et al. 2009; Shanee 2011; this volume; Shanee and Shanee 2011a, b; Shanee et al. 2007, 2013).

Our studies in Colombia have mostly used the taxonomy of Fooden (1963), even though recent doubts suggested splitting the genus *Lagothrix* into four species (Groves 2001, 2005). This view was accepted by many (e.g. Rylands and Mittermeier 2009, 2013; Mantilla-Meluk 2013) and rejected by others who have generated data aimed at rejecting the *Lagothrix* four-species hypothesis (Ruiz-Garcia and Pinedo-Castro 2009; Botero et al. 2010; Botero and Stevenson this volume; Defler this volume). Groves (2001, 2005) also placed the yellow-tailed woolly monkey into the genus *Oreonax* Thomas, 1927, although the validity of the use of *Oreonax* has been questioned and molecular data have been generated to reject this hypothesis (Matthews and Rosenberger 2008; Rosenberger and Matthews 2008; Cornejo et al. 2009).

This book is a continuation of our efforts to know more about this beautiful primate and to raise awareness about its threat of extinction. Many dedicated people have been working with this primate and especially a group of Stevenson's students coordinated by him have made great contributions in Colombia. Besides the field research, there is a lot happening in taxonomy and conservation. This is a very heterogenous primate species with widely divergent phenotypes and traces of an ancient history in *L. l. lugens,* while *L. l. lagothricha* seems to be much more recently evolved (Ruiz-Garcia and Pinedo-Castro 2009). The widely divergent phenotypes make it difficult to define the taxa that we call subspecies (Defler this volume) and introgression has been detected in two genetic studies (Ruiz-Garcia and Pineo-Castro 2009; Botero and Stevenson this volume) so that it is clear that these are not genetically separate taxa. For these reasons and the current evidence, we adopt the taxonomic approach proposed by Fooden (1963) in this book, in which there are two species of woolly monkeys, *L. lagothricha* and *L. flavicauda,* and the former divided into four subspecies.

In addition, from captive studies we know that these animals are very difficult to maintain healthily in captivity (Burns this volume) and the reproductive rates are slow (Mooney and Lee 1997; Nishimura 2003). A long-term breeding and exhibition project at the St Louis Zoo has generated a great deal of data on health and behavioral aspects, while dietary requirements have also been studied on several captive groups (White et al. 2010, this volume; Ange-van Heugten 2010, this volume; Ange-van Heugten et al. 2008, 2009).

1.1 Organization of the Volume

We have divided this book into five sections: Part I: Introduction; Part II: Systematics and Taxonomy; Part III: Ex Situ Research; Part IV: In Situ Ecology and Behavior; and Part V: Conservation.

1.1.1 Part I: Introduction: Historical Bibliography, Taxonomy, and Background for Woolly Monkey Studies

Here, we try to mention the most relevant field studies and some laboratory studies that form a background to this book and to our knowledge of woolly monkeys. We hope that we can show that already a great effort has been invested in these studies. Interestingly, these efforts have especially been centered in Colombia and the editors have been deeply involved in this research.

1.1.2 Part II: Systematics and Taxonomy

This section has two articles, both of which conclude that *L. lagothricha* is made up of four subspecies. These studies do not accept the recent splitting into two species for Colombia and thus these taxa in the country should be treated as subspecies (*L. l. lagothricha* and *L. l. lugens*).

Chapter 2 Botero and Stevenson used mitochondrial DNA to measure gene flow between the two putative species *lugens* and *lagothricha*. They determined cytogenetics and molecular markers by processing *Lagothrix* fecal samples from six sites, three in the historically defined distribution of *lugens* and three from sites in historically defined *lagothricha* distribution (Fooden 1963; Hernandez-Camacho and Cooper 1976).

Chapter 3 Defler conducted a broad geographic analysis of *Lagothrix* coat phenotypes and disagrees with Groves (2001) that the two recognized Colombian taxa are sharply distinct. He illustrates the multiple color variations in both *lugens* and *lagothricha* and states that there are no real diagnostic characters for these taxa aside from *lugens* being generally darker brown and gray as compared to *lagothricha* that is lighter brown and gray. He shows that there are exceptions even to this and that other characters used by Fooden and Groves to distinguish one taxon are to be found in the other taxon, and he concludes that these two taxa should be considered subspecies of *L. lagothricha*. Defler also considers a recent publication by Mantilla-Meluk (2013) that defined two more subspecies within the *lugens* taxon, which the author accepted as a species, *L. lugens*. He concludes that, because of the great variability of *lugens* phenotypes and the limited analyses carried out, limited to three local populations, it is impossible to recognize the taxa that were established in the article.

1.1.3 Part III: Ex Situ Research

Chapter 4 This is a very interesting case history of the behavior and husbandry of a captive group of woolly monkeys at the Louisville Zoo. In this chapter, Brent C. White and Silvia Zirkelbach, who have worked with this captive group since 1985, review the successful breeding that has occurred in this group as well as their analysis of stress using cortisol secretion with reference to age, sex, pregnancy, human visitors, and social behavior. They analyzed various social behaviors including a bachelor's group, social greetings, and social proximity and compared all of this to known wild behaviors. Since woolly monkeys are known to be very difficult to maintain in captivity and are prone to stress and to their related sequelae of kidney and heart problems, and high blood pressure, this information is invaluable for the future husbandry of the woolly monkey.

Chapter 5 Roy Burns, the Head Veterinarian of the Louisville Zoo, outlines the clinical experience and diseases of this well-known group of woolly monkeys and he provides an analysis of the impact of a viral disease that almost wiped out this captive group of 12 animals in 1996. Although it was impossible to identify the virus that was responsible, the suspicion is that it was a live polio virus transmitted through a backed-up sewer system that overflowed into the monkey building. Preventative health care for these animals is described in detail in this article as well as other health problems that have been treated over the years.

Chapter 6 Kimberley Ange shows that an inadequate diet and stress may contribute to the difficulty of managing woolly monkeys in captivity. By increasing insulin-type fructans in woolly diets, fecal cortisol levels were reduced as opposed to a diet rich in total carbohydrate, total sugar, glucose, and fruit content which showed high cortisol levels. She concludes that a reduction of stress and of improper nutrition in the maintenance of captive woolly monkeys could improve success in the maintenance of captive woolly monkeys. This is a powerful conclusion for a species that is difficult to maintain.

Chapter 7 Guzman and Stevenson examine the effect of housing conditions and diet on the expression of natural behaviors (using general activity profiles). They analyzed 14 enclosures for the above three factors, taking into account its size (including useable substrates at different levels), density of individuals, density per cubic meter, and an index of environmental enrichment. They found that environmental enrichment (especially the provision of many different levels of substrate) and a high-volume diet, allowing extended eating throughout the day (foraging), tended to produce behaviors that were more comparable to animals in the wild.

1.1.4 Part IV: In Situ Ecology and Behavior

Chapter 8 Christopher Schmitt and Anthony Di Fiore studied the behavior of juvenile and adolescent lowland woolly monkeys (*L. l. poeppigii*) in the Ecuadoran Amazon using three habituated groups for data collection. They found that young males preferentially associated with adult males and that young females were less social, especially before dispersal from the group. Just before dispersal, these females displayed a sharp increase in sexual interest in group males. The data of these two authors suggest that this age cohort (i.e. juveniles and adolescents) of woolly monkeys might be profitably studied in the future.

Chapter 9 Marcos Gonzalez and Pablo Stevenson describe seed dispersal in two woolly monkey groups at the Caparú Biological Station in eastern Colombia. They analyzed 1,397 fecal deposits and found 93,917 seeds belonging to at least 118 plant species. They calculated that a woolly monkey defecates on average 15 times a day, dispersing about 6,822 seeds per day. The mean dispersal distance was 577 m and germination experiments showed higher germination in seeds that had passed through an animal. The data confirm the woolly monkey as an important forest disperser that helps maintain plant diversity. Absence of the woolly monkey will allow a forest to decline in diversity.

Chapter 10 Sam Shanee studied ranging behavior, daily path lengths, diet, and habitat use in the critically endangered and endemic Peruvian yellow-tailed woolly monkey (*Lagothrix flavicauda*) during 15 months. He found variable home ranges between 95 and 147 ha, according to rainy or dry season. He measured path lengths between 1.03 and 1.2 km and identified 16 plant species in the diet. Leaf consumption increased during the dry season. These were among the smallest home ranges recorded for woolly monkeys. Their ability to survive in high densities in multiple types of habitat, including disturbed habitat, is important for their survival in the future.

Chapter 11 Julián León and companions studied the vocal communication of woolly monkeys (*L. l. lugens*) at Cueva de los Guacharos National Park in Colombia. This was the first acoustic analysis of vocalization in the species. They found differences in call rates between highland and lowland groups and individual differences in calls that might allow the individual to be recognized by other members of the group. Time of day, activity, age, and sex had strong influences on vocalization. Age and sex affected the structure of the calls.

Chapter 12 Pablo Stevenson examined the variation in woolly monkeys across 50 neotropical sites and studied variation in fruit production, climatic parameters, plant composition, and primate assemblages. He found that rainfall, number of dry months, and plant species richness were important factors at the largest spatial scale (regional). At a smaller scale (local), fruit abundance and the abundance of key resources affected woolly abundance.

Chapter 13 Diego Zárate and Pablo Stevenson studied the behavioral ecology and interindividual distances of woolly moneys in a rainforest fragment in Colombia because the species has been considered vulnerable to forest fragmentation. They found that activity patterns, diet, and spatial use of their study group were similar to woolly groups studied in unbroken forest. They also found a negative correlation between interindividual distances and group size and concluded that woolly monkeys in fragments are at danger only when the forest is not sufficiently productive to support the group and when hunting pressure becomes unsustainable for group numbers. Hunting primates in fragments has been shown to be easier than in wide expanses of forest.

1.1.5 Part V Conservation

Chapter 14 Diego Lizcano and companions carried out a population viability analysis of *lugens* woolly monkeys in western Amazonia, since that taxon has been given a critically endangered status (CR) in the International Union for Conservation of Nature (IUCN) system of species evaluation. The authors use multiple years of data collected by Akisato Nishimura from 1987 to 2002 in Tinigua National Park to construct stage-structured models to estimate population parameters. They showed that the female woolly monkeys contributed the most to population growth in this population and that any hunting of female woolly monkeys disproportionately affects population dynamics and would cause eventual population collapse should hunting remove more than 2% of the females from that population. The prevalence of face-whitened disease has a minor effect on population growth but could become an important negative factor over time.

Chapter 15 Juan Millán, Sara Bennett, and Pablo Stevenson studied the process of rehabilitation of woolly monkeys to an Amazonian forest habitat. They followed the progress of a small group of formerly captive animals as they became accustomed to a natural forest habitat and the authors collected behavioral data to compare with the same type of data collected from wild populations. These researchers described problems that were encountered during the rehabilitation of the animals and made suggestions for future attempts. Although the rehabilitation of woolly monkeys requires many hours of dedication to human care and monitoring, they suggest that rehabilitation and release may be an effective strategy for woolly monkey conservation.

Chapter 16 Noga and Sam Shanee reviewed the conservation status, anthropogenic threats, and conservation initiatives recognized and developed for the critically endangered Peruvian yellow-tailed woolly monkey *L. flavicauda.* Yellow-tailed woolly monkeys are impacted by habitat loss (agricultural expansion), hunting, selective logging, road construction, extractive industry, stochastic events, and climate change, which are increasing over the distribution of this species. Nevertheless, the yellow-tailed woolly monkey shows a strong ability to survive in disturbed forests. Population size and habitat are decreasing and will likely increase. Private sector land conservation is the most important conservation action, especially of local, rural communities. The authors suggest that the best strategy for protecting this woolly monkey is a combination of private efforts combined with landscape-level conservation.

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Part II
Systematics and Taxonomy

Chapter 2
Coat Color is not an Indicator of Subspecies Identity in Colombian Woolly Monkeys

Sergio Botero and Pablo R. Stevenson

Abstract Woolly monkeys are severely threatened, and disagreement on their taxonomic status complicates conservation strategies. Two subspecies of woolly monkeys inhabit Colombia, but the genetics of their populations have not been studied. Using mitochondrial DNA sequences, we set out to estimate the level of gene flow between populations, and to corroborate their taxonomic position. We found two separate evolving units with limited levels of gene flow. However, their separation does not correlate with the existing subspecies distinction, which is based on pelage color. We, therefore, propose a genetic differentiation of the woolly monkey taxa and emphasize the importance of the detected inconsistency in subspecies differentiation based on coat color.

Keywords *Lagothrix lagothricha lugens* · Platyrrhini · Pleistocene refugia · Primate conservation · Neotropical primates · Atelidae · Atelinae

2.1 Introduction

Woolly monkeys (*Lagothrix*, Atelidae) are important seed dispersers in the ecosystems they inhabit (Di Fiore and Rodman 2001; Nishimura 1999; Peres 1996; Stevenson 2000), dispersing over one third of the effectively dispersed seed biomass in forests where they are abundant (Stevenson 2007). Woolly monkeys are threatened by habitat destruction and hunting, both for their meat and local pet trade (Boubli et al. 2008; Stevenson et al. 2008; Peres and Palacios 2007). The Andean populations are the most threatened, and this situation is further aggravated by uncertainty regarding the taxonomic status of its taxa (Defler 2004).

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The taxonomy of the genus was originally revisited in 1963, when it was determined that woolly monkeys comprised two species, *Lagothrix flavicauda* and *Lagothrix lagothricha*. The latter was also subdivided into four subspecies: *L. l. lugens, L. l. lagothricha, L. l. cana,* and *L. l. poeppigii* (Fooden 1963). This taxonomy remained unchanged until 2001 when, based on morphological characters of museum specimens, all the taxa were raised by a level, separating the group into two genera: *Oreonax* and *Lagothrix*. *Oreonax* is a monotypic genus with *Lagothrix flavicauda* as its only species, and *Lagothrix* is now composed of four species: *L. lugens, L. lagothricha, L. cana,* and *L. poeppigii* (Groves 2001). The proposal of *Oreonax* has been shown to be an artifact of sampling (Matthews and Rosenberger 2008), and it is likely that the subspecies status is a better description of the remaining taxa (Defler 2004). To avoid ambiguity, we will use Fooden's (1963) taxonomy for the rest of the paper.

There are two taxa of woolly monkeys in Colombia (Fig. 2.1). *L. l. lagothricha* inhabits the south of the country in southern llanos, the Amazon region, and its range extends well into the Amazonas of neighboring countries. It has been classified by the International Union for Conservation of Nature (IUCN) as Vulnerable due to low natural densities, hunting pressure, and habitat degradation, although its wide range and presence in some pristine areas make it of minor concern when compared to other taxa in the group (Palacios et al. 2008). *L. l. lugens* inhabits the eastern and central cordilleras in the northern Andes and adjacent lowlands, showing the smallest distribution of all subspecies. It is likely extinct in Venezuela and is considered Critically Endangered due to both habitat degradation and hunting (Stevenson and Link 2008). The diagnostic difference between the taxa is a uniform brown color for *L. l. lagothricha* and a black to gray color for *L. l. lugens,* although significant variation in coat color is described in the classic revision (Fooden 1963) and recent reviews (Defler 2004).

With the use of molecular and cytogenetic markers, *L. l. lugens* and *L. l. lagothricha* were previously shown to be nonreciprocally monophyletic, rejecting their previously proposed species status (Botero et al. 2010). However, these analyses did not incorporate geographical information, precluding a detailed interpretation of the demographical processes between the subspecies, and the sample origin was assigned based exclusively on coat color. Here, we set out to corroborate these results, while including geographical information by sampling several of the Colombian populations of woolly monkeys.

2.2 Methods

Fecal samples of six populations of woolly monkeys were collected in 99 % ethanol during a period from June 2008 to August 2009. We only report the samples that effectively amplified during the polymerase chain reactions (PCRs) performed, as the number of samples collected per population varied significantly. Sampling sites are indicated in Fig. 2.1. Sampling site coordinates, taxa, phenotype observed, and

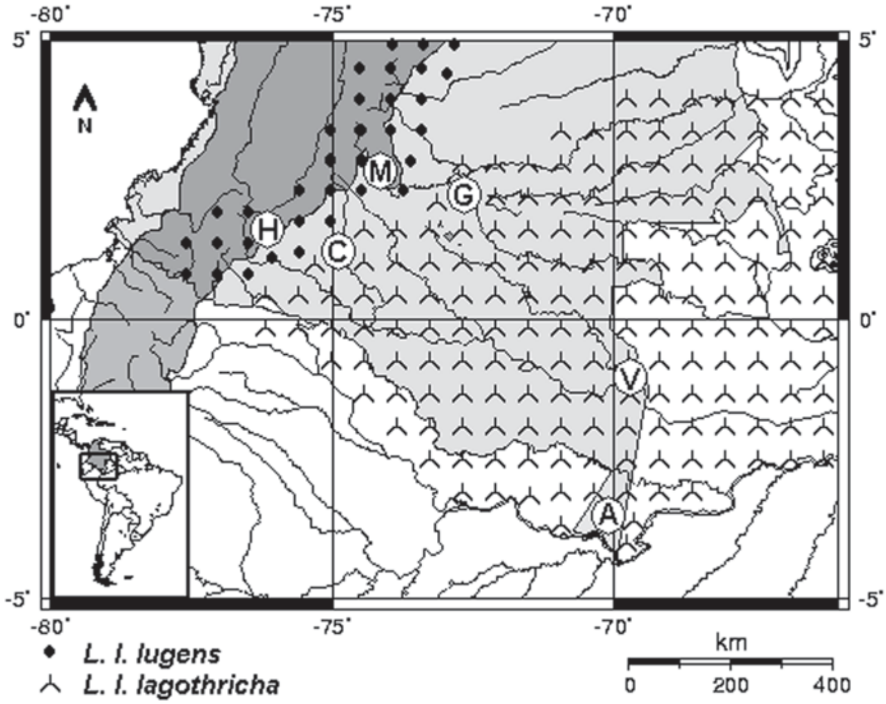

Fig. 2.1 Map showing the location of sampling sites in Colombia (country limits outlined in *light gray*). *A*, Amazonas; *V*, Vaupés; *C*, Caquetá; *H*, Huila; *G*, Guaviare; *M*, Meta. The major rivers (*black*) and the 700 m above sea level isocline (*darkest gray* inside of Colombia, *dark gray* outside) are outlined. Map obtained with the online GMT implementation. (Wessel and Smith 1991)

sample size are provided in Table 2.1. For the Estación Biológica Caparú population, samples were collected for a previous study unrelated to the current one. Coordinates should only be used as an approximation since the samples were gathered during extensive follow-ups and the coordinates given correspond to the location of the housing facilities in each site. In all cases, the coat color of the individuals sampled corresponded to that of the subspecies assigned based on their geographical location.

DNA was extracted using QIAamp DNA Stool Mini Kit (Qiagen) or UltraClean Fecal DNA Isolation Kit (MoBio) according to manufacturer protocols. After extraction, we amplified the hypervariable region I of the mitochondrial D-loop region in a total volume of 50 µl using 1X reaction buffer, 2.5 mM magnesium chloride, 0.8 mM dNTP (Bioline) each, 0.5 µM primer each, 2.5 uBiolase DNA Polymerase (Bioline), and 0.1 µg/µl BSA (Promega). Thermal profile consisted of an initial denaturation at 94 °C, 10 min; followed by 47 cycles of 94 °C, 30 s; 60 °C, 45 s; 72 °C, 45 s; and a final extension at 72 °C for 7 min, with primers L15400 (5′-TCCACCATTAGCACCCAAAG-3′) and H15940 (5′-CCTGAAGTCGGAACCAGATG-3′), which had been used previously on atelines (Collins and Dubach 2000) and the nomenclature by Kocher et al. (1989) was followed. We checked successful

Table 2.1 Sampling sites coordinates and sample sizes

Site	Coordinates	Taxa	Coat color	*N*	Code in figures
Serranía de la Macarena Parque Nacional Natural (PNN) Tinigua in the eastern cordillera piedmont in Meta	2° 37′N, 74° 4′W	*L. l. lugens*	Gray	17	M
PNN Cueva de los Guacharos, at the base of the eastern cordillera in Huila	1° 36′N, 76° 6′W	*L. l. lugens*	Gray	11	H
Caquetá on the western bank of the Caguan river, in the eastern cordillera piedmont. This is a small remnant population in a heavily degraded landscape	1° 20′N, 74° 53′W	*L. l. lugens*	Gray	9	C
PNN Amacayacu, on the northern bank of the Amazonas river, near the city of Leticia, in Amazonas	3° 23′S, 70° 9′W	*L. l. lagothricha*	Brown	16	A
Granja de Investigaciones "El Trueno," Instituto SINCHI, at the border between the Orinoquia and Amazonia region in Guaviare	2° 22′N, 72° 41′ W	*L. l. lagothricha*	Brown	9	G
Estación Biológica Caparú in Vaupés	1° 4′S, 69° 30′W	*L. l. lagothricha*	Brown	10	V

amplification of a ~490-bp band on 1 % agarose gels, and sequenced positive reactions though Macrogen Korea commercial service. Only the sequencing reactions were outsourced; every other step in the processing of samples was performed in our laboratory. Sequences have been deposited in GenBank under accession numbers: GU212746-GU212756 Huila, GU212728-GU212736 Caquetá, GU212774-GU212783 Vaupés, GU212757-GU212773 Meta, GU212712-GU212727 Amazonas, and GU212737-GU212745 Guaviare.

As a minimum, three different sequencing reactions, from different PCRs, were performed for each primer. We only report results on samples that showed high-quality amplifications to avoid including nuclear integrations of mitochondrial DNAs (NUMTs) in the study. Since the region studied does not code for a protein, it is not possible to translate the DNA sequence into an amino acid sequence to detect premature stop codons as possible indicator of a NUMT. However, due to the probabilistic nature of PCR, and the relatively high amount of mitochondrial genome copies per cell (about 1,000–10,000; Shadel and Clayton 1997), it would be highly unlikely to find only homozygous individuals should the primers used anneal on one or more NUMTs. This assumption should hold even if the primers preferentially align on the NUMTs, a scenario that must be contemplated given that they were derived to anneal on conserved regions of the D-loop (Collins and Dubach 2000). Considering the relatively high number of haplotypes found in our study, heterozygous individuals should be expected if NUMTs were included. We thus believe our data to be free of NUMTs, but the inclusion of NUMTs cannot be completely ruled out.

Sequences were aligned using ClustalW (Larkin et al. 2007), as implemented in Bioedit (Hall 1999), and trimmed at the ends for a final sequence length of 431 nucleotides which included no gaps. For phylogenetic analyses, we performed maximum parsimony (MP) and maximum likelihood (ML) heuristic searches in PAUP* 4.0b10 (Swofford 2003). Parameters of the searches were 1,000 random addition sequence replications keeping ten trees per cycle for MP, and ten random addition sequence replications keeping ten trees per cycle using the TPM1uf + I model, as selected using jModelTest (Posada 2008; Guindon and Gascuel 2003) with the Bayesian information criterion (BIC). Bootstrap support was obtained with 1,000 replicates for MP and 100 for ML. We performed a Bayesian phylogenetic inference analysis in MrBayes 3.2.1 (Ronquist and Huelsenbeck 2003). The parameters used were seven Markov Chain Monte-Carlo (MCMC) runs, 1,000,000 steps long each, a burn-in fraction of 0.5, the TPM1uf + I model, and all others set to default. The use of seven chains ensures that swapping between them is high, effectively providing good sampling of the space. For comparison of the tree topologies obtained, we used a Shimodaira–Hasegawa (SH) test (Shimodaira and Hasegawa 1999) with 1,000 bootstrap replicates, as implemented in PAUP* (Swofford 2003). We did not use out-groups for the analysis because the high mutation rate of the mitochondrial marker used would confound the analysis since saturation is likely to be a problem (Pesole et al. 1999). This was evident when an alignment was made using *Ateles* as an out-group, requiring several gaps and showing regions in which it was impossible to find an unequivocal alignment.

For demographic analysis, we used the program DNAsp v5.00.07 (Rozas et al. 2003) to estimate basic statistics as well as Fs (Fu 1997) and R2 (Ramos-Onsins and Rozas 2002), with a coalescent confidence interval calculated with 10,000 replicates. We used the program Arlequin v3.1 (Excoffier et al. 2005) to perform an analysis of molecular variance (AMOVA), with 10,000 permutations, to determine the population structure. Pairwise F_{st} between populations were also calculated to estimate the effective number of migrants per generation (Nm) with the equation $F_{st} = (2\mathrm{Nm} + 1)^{-1}$, with 1,000 permutations to obtain a significance estimator. We tested the hypothesis of isolation by distance between populations with a Mantel test in the same program, using a distance matrix calculated in hundreds of kilometers (100 km) and 10,000 permutations. We constructed a haplotype network in the program Network (Fluxus engineering), using a median-joining algorithm (Bandelt et al. 1999).

We used a coalescent approach to estimate the time of separation, and the level of gene flow between the subspecies. Specifically, we tested for an isolation with migration model (Nielsen and Wakeley 2001), as implemented in the program IM (Hey and Nielsen 2007). This model assumes each population is constant in size. For this analysis, we used ten MCMC chains of 70,000,000 steps, sampling every 100 steps, with a burn-in of 350,000 steps, and a geometric heating scheme with parameters $h_1 = 0.8$ and $h_2 = 0.9$. After seven optimization runs, we defined values of 400 for the q_1 parameter: 1 for the t parameter and maximum values of 2 and 1 for the m_1 and m_2 parameters, respectively. These parameters allowed us to achieve maximum sampling of the space near the peak values. We checked the probability plots and autocorrelation plots to evaluate the convergence of the parameters.