Developments in Primatology: Progress and Prospects
Series Editor: Louise Barrett

Thomas R. Defler
Pablo R. Stevenson *Editors*

The Woolly Monkey

Behavior, Ecology, Systematics, and Captive Research

Springer

The Woolly Monkey

Developments in Primatology: Progress and Prospects

Series Editor

Louise Barrett, *Department of Psychology, University of Lethbridge, Lethbridge, Alberta, Canada*

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Thomas R. Defler • Pablo R. Stevenson
Editors

The Woolly Monkey

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Editors
Thomas R. Defler
Departamento de Biología
Universidad Nacional de Colombia
Bogotá
Cundinamarca
Colombia

Pablo R. Stevenson
Ciencias Biologicas
Universidad de Los Andes
Bogotá
Colombia

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Contributors

Jorge A. Ahumada Conservation International, Arlington, VA, USA

Kimberly D. Ange-van Heugten North Carolina State University, Raleigh, NC, USA

Sara E Bennett Fundación Maikuchiga, Bogotá, Amazonas, Colombia

Sergio Botero Laboratorio de Ecología de Bosques Tropicales y Primatología (LEBTYP), Universidad de los Andes, Bogotá, Colombia

Rockefeller University, New York, NY, USA

Roy Burns Louisville Zoological Garden, Louisville, USA

Edgar F. Cifuentes Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Thomas R. Defler Departamento de Biología, Universidad Nacional de Colombia, Bogotá, Colombia

Anthony Di Fiore Department of Anthropology, University of Texas, Austin, TX, USA

Nelson F. Galvis Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Marcos González Centro de Investigaciones Ecológicas La Macarena, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Diana Carolina Guzmán-Caro Universidad de Los Andes, Bogotá, Colombia

J. Julián León Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Diego J. Lizcano Grupo de Investigación en Ecología y Biogeografía (GIEB), Universidad de Pamplona, Pamplona, Norte de Santander, Colombia

Juan F Millán Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá and Fundación Maikuchiga, Bogotá, Amazonas, Colombia

Akisato Nishimura Doshisha University, Kyotanabe, Kyoto, Japan

Centro de Investigaciones Ecológicas La Macarena (CIEM), Universidad de los Andes, Bogotá, Colombia

Mónica A. Ramírez Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Christopher A. Schmitt Center for Neurobehavioral Genetics, Semel Institute for Neuroscience and Human Behavior, University of California, Los Angeles, CA, USA

Noga Shanee Neotropical Primate Conservation, Manchester, UK

Sam Shanee Neotropical Primate Conservation, Manchester, UK

Pablo R. Stevenson Departamento de Ciencias Biológicas, Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los Andes, Bogotá, Colombia

Departamento de Ciencias Biológicas, Centro de Investigaciones Ecológicas La Macarena, Universidad de Los Andes, Bogotá, Colombia

Sergio A. Vargas Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

Brent C White Centre College, Danville, USA

Diego A. Zárate Departamento de Ciencias Biológicas, Centro de Investigaciones Ecológicas La Macarena, Universidad de Los Andes, Bogotá, Colombia

Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, México City, México

Silvia Zirkelbach Louisville Zoo, Louisville, USA

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.

T. R. Defler (✉)
Departamento de Biología, Universidad Nacional de Colombia, Bogotá, Colombia
e-mail: thomasdefler@gmail.com

P. R. Stevenson
Laboratorio de Ecología de Bosques Tropicales y Primatología (LEBTYP),
Universidad de los Andes, Carrera 1 No 18a-10, Bogotá, Colombia
e-mail: pstevens@uniandes.edu.co

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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).

S. Botero (✉) · P. R. Stevenson
Laboratorio de Ecología de Bosques Tropicales y Primatología (LEBTYP),
Universidad de los Andes, Carrera 1 No 18a-10, Bogotá, Colombia

S. Botero
Rockefeller University, 1230 York Avenue, Box 18, New York, NY 10065, USA
e-mail: sbotero@rockefeller.edu

P. R. Stevenson
e-mail: pstevens@uniandes.edu.co

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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

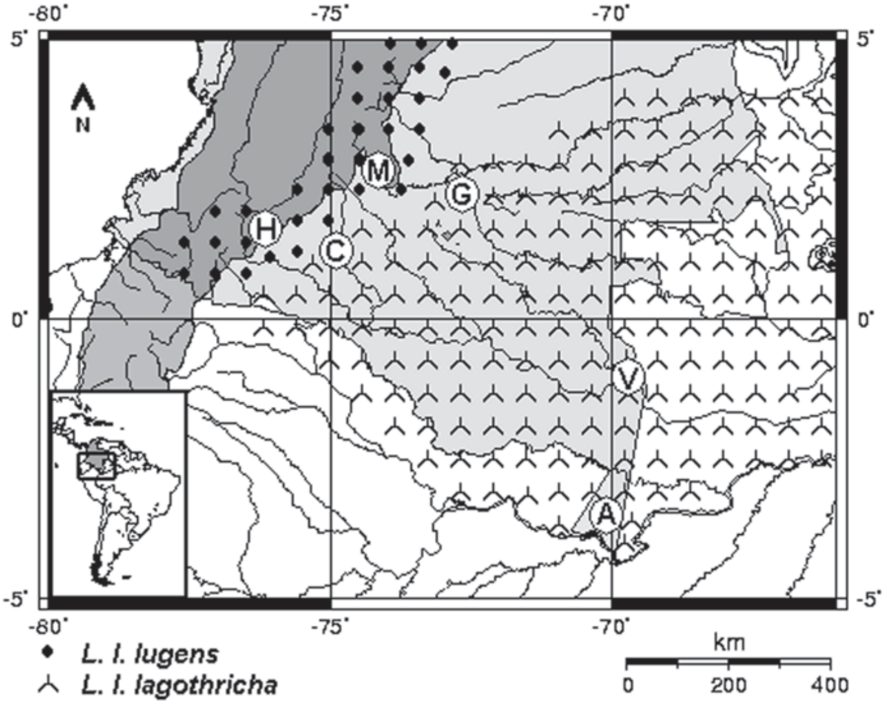

Fig. 2.1 Map showing the location of sampling sites in Colombia (country limits outlined in *light gray*). *A*, Amazonas; *V*, Vaupés; *C*, Caquetá; *H*, Huila; *G*, Guaviare; *M*, Meta. The major rivers (*black*) and the 700 m above sea level isocline (*darkest gray* inside of Colombia, *dark gray*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

The mutation rate used for our time of separation analysis, 19.4×10^{-9} mutations per site per year, comes from the average D-loop extended termination-associated sequences (ETAS) domain (which encompasses the hypervariable region I) as estimated for closely related pairs of mammals (Pesole et al. 1999). The highly variable D-loop region is ideal to resolve the phylogeny of very closely related taxa (Whittaker et al. 2007), but its high mutation rate makes its use for a molecular clock complicated, and it can vary significantly between similar taxa (Pesole et al. 1999). Amplification of other mitochondrial markers, for which more precise mutation rates are known or could be determined, failed for our samples (for COI, COII, and cytB a large proportion of samples did not amplify or showed very noisy chromatograms suggesting amplification of NUMTs, data not shown). Given the lack of better data, we opted for using the average mutation rate determined by Pesole and coworkers, which is also quite close to that of the *Homo–Pan* comparisons (while smaller than that of the *Pan paniscus–Pan troglodytes* comparison; Pesole et al. 1999). The estimated values of separation time are thus an approximation and should be treated with caution.

We repeated the AMOVA and IM analysis (which are the only ones done between subspecies and not populations), grouping the Guaviare population with *L. l. lugens*, since we propose this as a better grouping (see results and discussion). We changed the IM *t* maximum parameter to 35, and the number of steps to 100,000,000, with a burn-in of 500,000 to achieve convergence and a large effective sample size. These parameters were determined after four optimization runs.

2.3 Results

The number of haplotypes, the nucleotide diversity (Pi), and the number of segregating sites for each population and subspecies are given in Table 2.2. Phylogenetic analyses did not show reciprocal monophyly between the subspecies and coat color does not differentiate any clades. The obtained tree topologies were similar and depicted alternative relationships were not rejected (SH test $p > 0.05$ for all possible combinations). The phylogram obtained for the Bayesian inference analysis is shown in Fig. 2.2, indicating node support for the other analysis when nodes were shared.

Demographic analyses showed no evidence of population size changes for *L. l. lagothricha* (Fs = −2.19, 95 % confidence interval (CI): −7.73–5.96, $P = 0.24$; $R_2 = 0.18$, 95 % CI: 0.06–0.17, $P = 0.99$), or *L. l. lugens* (Fs = 1.34, 95 % CI: −6.25–6.54, $P = 0.73$; $R_2 = 0.12$, 95 % CI: 0.06–0.18, $P = 0.56$). This also holds for *L. lagothricha* as a species (Fs = −2.14, 95 % CI: −10.1–9.51, $P = 0.31$; $R_2 = 0.16$, 95 % CI: 0.05–0.16, $P = 0.98$). AMOVA results showed no significant separation between the subspecies ($F_{ct} = 0.28$, $P = 0.30$), while significant population structuring did exist ($F_{st} = 0.63$, $P < 0.000001$). When the analyses are performed, including the Guaviare population in the *L. l. lugens* taxon instead of considering it as *L. l. lagothricha,* significant population structure ($F_{st} = 0.70$, $P < 0.000001$) as well as significant separation between the taxa ($F_{ct} = 0.62$, $P = 0.047$) are detected.

Table 2.2 Descriptive genetic diversity statistics for the sampled populations

Population	Phenotype	N	Pi	Number of haplotypes	Number of segregating sites
Amazonas	Brown	16	0.029	11	38
Guaviare	Brown	9	0.007	7	9
Vaupés	Brown	10	0.029	6	27
Caquetá	Gray	9	0.015	3	13
Huila	Gray	11	0.025	6	26
Meta	Gray	17	0.005	4	7
L. l. lagothricha	Brown	35	0.043	24	50
L. l. lugens	Gray	37	0.017	12	32
L. l. lagothricha[a]	Brown	26	0.031	17	43
L. l. lugens[a]	Gray and brown	46	0.015	17	33

[a] Results are given for the conventional subspecies as well as for the new grouping we propose (see discussion)

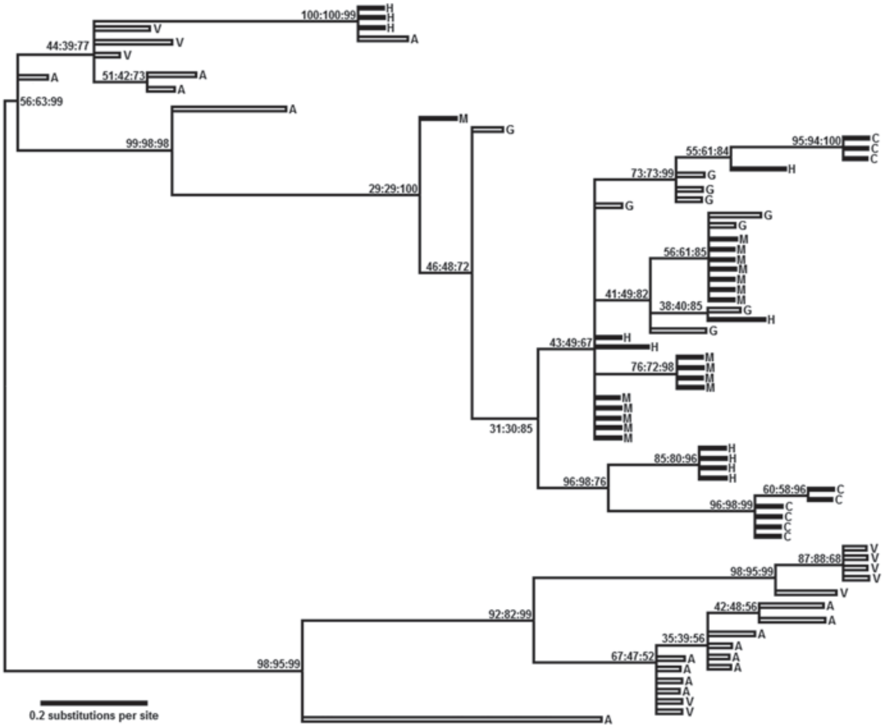

Fig. 2.2 Phylogram obtained in the Bayesian inference analysis. Node support is indicated when nodes are shared between trees obtained in the analysis (MP|ML|Bayesian inference posterior probability *100). A, Amazonas; V, Vaupés; C, Caquetá; H, Huila; G, Guaviare; M, Meta. *Solid thick* terminals represent gray phenotypes, *while hollow* ones represent brown phenotypes. Note that the tree is unrooted

Table 2.3 Estimated values of effective number of migrants per generation (Nm) between populations included in the study

Population	Caquetá	Meta	Huila	Guaviare	Amazonas
Meta	0.53^{***}	–	–	–	–
Huila	2.41^{*}	1.28^{***}	–	–	–
Guaviare	0.92^{**}	6.29	2.20^{*}	–	–
Amazonas	0.30^{***}	0.18^{***}	0.43^{***}	0.23^{***}	–
Vaupes	0.26^{***}	0.14^{***}	0.39^{***}	0.19^{***}	3.13^{*}

Note the P values are derived from F_{st} calculations (see "Methods"), thus a nonsignificant value indicates enough migration between the populations as to make them undistinguishable genetically when analyzing their D-loop sequences (F_{st} nonsignificantly different from 0)
* $P<0.05$; ** $P<0.01$; *** $P<0.001$

The obtained values of Nm are given in Table 2.3. These values come from the estimated F_{st} between pairs of populations, which showed significant results in all cases ($P<0.05$) except for the Meta–Guaviare populations, which would be undistinguishable. This approach to calculate Nm has drawbacks, but it is adequate when distance is assumed to be the main factor for population structure and Nm values are small (Holsinger and Weir 2009). There is considerable gene flow in populations of the same subspecies, with the exception of the *L. l. lagothricha* Guaviare population, which shows limited gene flow with other *L. l. lagothricha* populations while showing very high gene flow with *L. l. lugens* populations. Inside *L. l. lugens,* only the Meta population shows reduced gene flow with the Caquetá population. Mantel test showed a marginally nonsignificant correlation of the genetic distance matrix with the geographic distance matrix ($r=0.78$, $P=0.056$, explained variance =61 %). The IM analysis estimated Nm value of 0.22 (95 % CI: 0.19–13.5) effective migrants per generation from *L. l. lagothricha* to *L. l. lugens* and of 5.6 (95 % CI: 0.91–51.4) effective migrants per generation in the opposite direction, which would indicate intermixing of the subspecies with a preferential gene flow from *L. l. lugens* to *L. l. lagothricha*. This is consistent with the levels of gene flow between pairs of populations estimated though the F_{st}. The relatively large confidence intervals obtained should not change the overall conclusion from the analysis since the trend of the values allows for a directional estimate of the migration, and a value of Nm higher than 0.5 is considered to indicate relatively high levels of gene flow (Hey 2010). Effective sampling size was above 800 for all parameters of the IM analysis.

When the Guaviare population is included as part of *L. l. lugens,* the estimated values of Nm also change, being now 0.016 (95 % CI: 0.05–4.1) effective migrants per generation from *L. l. lagothricha* to *L. l. lugens* and of 0.018 (95 % CI: 0.09–9.3) migrants per generation in the opposite direction. The distribution of the Nm values showed an ever-decreasing tendency, and this is reflected in the estimated value being outside of the 95 % confidence interval. Although this fact seems odd, it is to be expected, given that the confidence interval is calculated based on the posterior distribution of the values found, so the maximum value would always be outside of the confidence interval if the distribution is constantly decreasing. These values in-

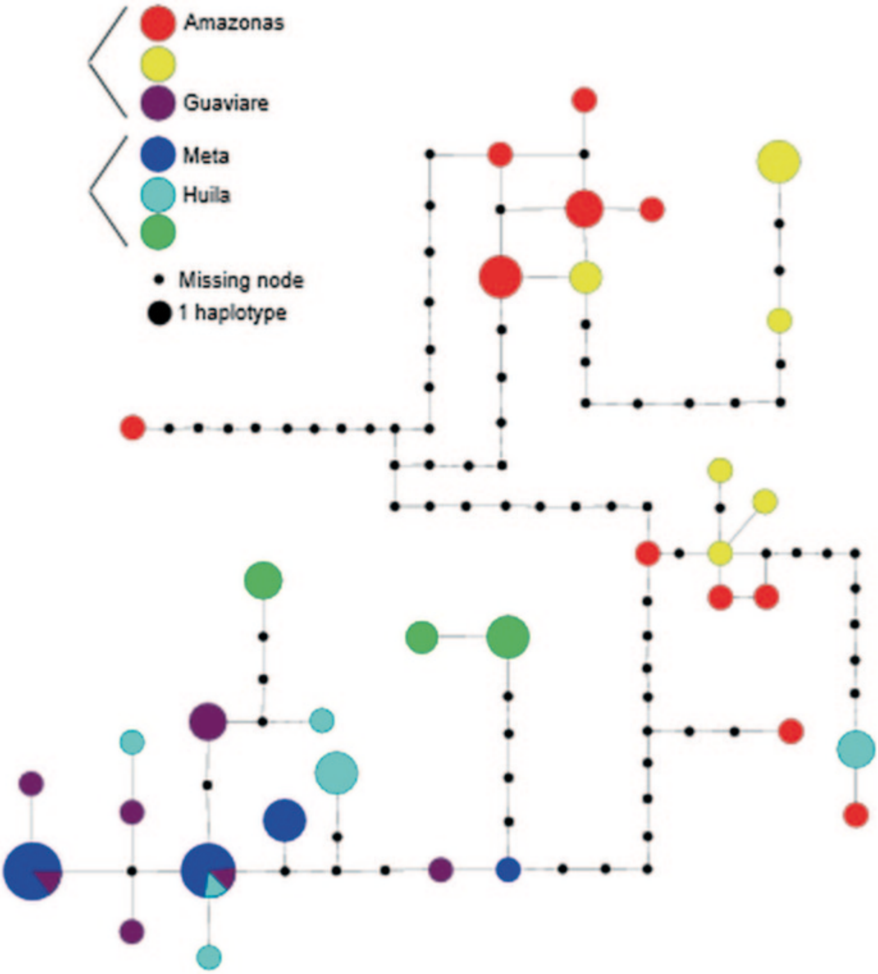

Fig. 2.3 Haplotype network for the sequences included in the analysis

dicate a very limited level of gene flow between the two subspecies if the grouping we propose is applied. Effective sampling sizes were above 2,500 for all parameters of the analysis.

After the optimization of the parameters, the probability plots and autocorrelation plots showed no abnormal behavior, suggesting a good sampling of the space in both IM analyses.

The constructed haplotype network is shown in Fig. 2.3. There is a general segregation of the two taxa, but the *L. l. lagothricha* Guaviare population is clearly mixed with the *L. l. lugens* populations. There are also some *L. l. lugens* individuals from the Huila population that are more closely related to the *L. l. lagothricha* populations. Overall, the network is consistent with the levels of gene flow and structure calculated.

The IM analysis estimates the time of separation of the subspecies including populations of Amazonas, Vaupes, and Guaviare in *L. l. lagothricha* and populations Meta, Caqueta, and Huila in *L. l. lugens* to be 50,649 years ago (95 % CI: 15,368–116,547) and 1,831,332 years ago (95 % CI: 546,260–4,095,904) when the Guaviare population is included in *L. l. lugens*.

2.4 Discussion

The absence of detectable demographic changes in the data represents a good starting point for other analyses, such as the Nm calculations, that assume a constant population size. It should be noted that this reflects an absence of population size changes several generations ago. Recent anthropogenic effects would not be detected under this analysis and are beyond the scope of this project. Our estimates of the migration level between populations seem to be realistic since we used a mitochondrial marker and, although there is some evidence of limited male dispersal in the species (Di Fiore and Fleischer 2005; Maldonado and Botero 2009), dispersal in the species is almost entirely by females (Nishimura 2003).

The observed absence of monophyly between the taxa evaluated is consistent with previous results that support a subspecies scheme (as opposed to separate species) in which there is some level of intermixing (Botero et al. 2010). However, that observation alone cannot distinguish between incomplete lineage sorting and true intermixing between the populations. The isolation with migration model used is ideal to approach this problem (Hey and Nielsen 2004; see below).

Estimated migration values show a high level of gene flow between the Caquetá and Huila populations, which is to be expected given their geographical proximity. It was unexpected to find *L. l. lugens* as far into the lowlands as we did in the Caquetá population, given the previously defined boundaries (Fooden 1963; Hernández-Camacho and Cooper 1976). A detailed study to determine the precise limits between the taxa is thus necessary. The Huila population also shows a high level of gene flow with the Meta population, while the Caquetá population shows reduced gene flow with the later. High levels of gene flow are observed between the *L. l. lagothricha* Amazonas and Vaupés populations, but the Guaviare population shows limited migration with these two populations while showing high levels of migration with the *L. l. lugens* populations. This is unexpected since the distribution of *L. l. lagothricha* appears to be continuous (Hernández-Camacho and Cooper 1976), and the phenotype of the Guaviare population is that of that subspecies.

The Mantel test results show a marginally nonsignificant relationship, which would agree with a proposed limited area of contact only in the Caquetá cordillera slope (Hernández-Camacho and Cooper 1976; Fooden 1963), since geographic distance would not be a good indicator of gene flow between the populations. However, the high levels of gene flow between the Guaviare and Macarena populations strongly suggest that this is not the case. A detailed analysis including several populations from Orinoquia and northern Amazonia regions would be necessary to determine if there is an environmental factor creating the separation between those populations or if in fact the separation is due purely to geographical distance isolation. The presence of *L. l. lugens* well into the lowlands of Caquetá also argues that the area of contact might be larger. These results, together with the migration estimates, suggest that the species is interbreeding, but that there is some unknown factor which limits the level of gene flow between the two subspecies. It should be noted then that the cordillera slope in the Caquetá region is not a limit between the distribution of the subspecies, but simply a contact area between the mountain and lowland populations.

The haplotype network is in agreement with the Nm values obtained, showing intermixing of the taxa and a clear association of the Guaviare population with the *L. l. lugens* populations. There seem to be two relatively distinct groups that do not resemble the proposed subspecies scheme because of the dissident Guaviare population. This might reflect a previous connection between the Meta and Guaviare population, and might thus be evidence of recent forest recession in the area, creating the boundary observed at present. It has previously been proposed that the Guaviare region, and more generally several areas of the Orinoquía region, would be forested if anthropogenic intervention had not occurred (Etter et al. 2006), and this is clearly in agreement with our results. We then propose that there are two independent evolving units, the Andean–Orinoquían populations and the Amazonian populations, which show some gene flow, but whose exact boundaries remain to be determined.

The time of separation between the subspecies had been previously estimated to be about 23,000 years with the use of both COII and D-loop hypervariable region I using the same isolation with migration model (Botero et al. 2010). The previous analysis had a small sample size and the mutation rate was higher for the D-loop, which should contribute to the smaller estimate (approximately 23,000 vs. 51,000 years). However, the confidence intervals obtained are quite similar (3,948–125,498 years previously vs. 15,368–116,547 years in this study), locating the separation of the subspecies sometime in the late Pleistocene to Holocene.

The increase in the estimated time since separation for the subspecies when the Guaviare population is included as part of *L. l. lugens* (approximately 1,800,000 years) displaces the event to the early to middle Pleistocene. The large confidence intervals obtained preclude more detailed inferences, although it is clear that it is significantly earlier as can be seen from the nonoverlapping CI for the two grouping schemes. The separation time, together with the low level of gene flow detected in the same analysis when this grouping is applied, supports the idea of two separately evolving taxa. This separation fits well with the subspecies status, but the taxa would not correspond with the morphological characters previously described.

Overall, our results do not support the previously proposed subspecies scheme based on coat color. While we find two generally independent evolving units, these do not correlate with the proposed coat color division (Fooden 1963), a fact that had already been questioned based on the presence of intermediate phenotypes (Defler 2004). We propose that the subspecies classification be revisited, since the current color-based determination does not accurately represent the level of segregation observed in natural populations.

A broader scale analysis including all the subspecies in *Lagothrix lagothricha* using only the COII region has been performed by Ruiz and Pinedo (2010). Absence of monophyly between the subspecies was observed and the time of separation between *L. l. lugens* and *L. l. lagothricha* was determined to be between 1 and 1.4 million years, which is slightly lower but in the same geological time (early Pleistocene) as our results when the Guaviare population is included as part of *L. l. lugens*.

A simulation study on the performance of the isolation with migration model suggests that the level of gene flow might be overestimated if the assumption of constant gene flow is not met (Becquet et al. 2009). This is of particular relevance for this study since forest regression and expansion could have occurred during the Pleistocene in the area (Hernández-Camacho et al. 1992). Although the extent of forest change is not clear, it would certainly affect the level of gene flow between populations. This would however not affect our taxonomic interpretation, since we propose that the level of gene flow is enough to maintain the subspecies status, but that the two taxa should be considered independent evolving units for conservation purposes.

Our study complements the previously published work (Botero et al. 2010; Ruiz-Garcia and Pinedo-Castro 2010) by doing a population-based analysis on a detailed geographical scale. Despite differences in the estimates, all these studies place the separation of *L. l. lugens* and *L. l. lagothricha* sometime during the Pleistocene period. However, all the studies to date have relied exclusively on mitochondrial markers and, except for the current work, the geographical information was inexistent (Botero et al. 2010) or too broad (Ruiz-Garcia and Pinedo-Castro 2010). Future analysis should try to increase the geographical detail and evaluate the levels of gene flow between populations with microsatellite or other nuclear markers which allow for higher resolution. Of special importance would be to determine the levels of gene flow, and potential barriers to it, that exist between the Orinoquia and Amazonia populations.

The *L. l. lugens* taxon seems then to be appropriately protected, since it is both present in the Parque Nacional Natural (PNN) "Cueva de los Guacharos" in Huila and the PNN "Tinigua" in Meta. However, the Guaviare population, which we propose is part of the taxon, is severely threatened, and is reduced to small forest fragments (Zarate and Stevenson 2010). Efforts should be made to preserve this population and identify other populations in the region, since they represent a unique arrangement in which to study the interactions between coat color and other genetic traits in *Lagothrix*. If our results are replicated using nuclear markers, coat color would no longer allow for distinction between the taxa, and the previously described geographical limits would not apply.

A recent paper treats *L. l. lugens* as a species and proposes subdividing it into several subspecies based on morphological variation that correlates with their geographical origin (Mantilla-Meluk 2013). This conclusion appears to us premature given that morphological characters do not seem to correlate well with genetic differentiation even at the gross *L. l. lugens*–*L. l. lagothricha* division based on color (Botero et al. 2010).We speculate that a significant proportion of the morphological variation normally observed in the genus might be due to phenotypic plasticity. Until more information on the population dynamics of *Lagothrix* becomes available, a molecular approach should be implemented when the origin of a primate in this genus is relevant for any purpose.

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Chapter 3
Colombian *Lagothrix*: Analysis of Their Phenotypes and Taxonomy

Thomas R. Defler

Abstract Colombian *Lagothrix* are phenotypically very complex and a clear diagnosis of the two taxa (that classically have been recognized for the country) does not exist. The characteristics used to define one taxon are often found in the other taxon. Only the *Lagothrix lugens* of the Central Cordillera of the Andes is clearly defined and different from all other populations despite the holotypic description. *Lagothrix* from the Eastern Cordillera, although generally darker than those found in the greater part of Amazonia (called *lagothricha*), have many characteristics that can be found also in *lagothricha*, such as coronal stripe and agouti back and forearms, while some *lagothricha* are also dark brown and gray like the majority of *lugens* of the Eastern Cordillera. Since the described taxa are not clearly distinct from each other, it seems more correct to see them as subspecies of a species *L. lagothricha,* which often intergrade with one another. Two other subspecies have recently been described from the east of the Eastern Cordillera, although it is not clear whether these newly defined subspecies include other populations of the former *lugens* from the east of the Andes. Populations called *lagothricha* and *lugens* seem to be made up of a mosaic of phenotypes with no clines. Genetic information supports the view of a polytypic, broadly distributed species, *L. lagothricha* with various distinctive populations, although further analysis might force us to abandon the subspecies of *L. lagothricha* in Colombia altogether.

Keywords *Lagothrix lagothricha* · *lugens* · Woolly monkey taxonomy in Colombia · Phenotypes · Taxonomy

3.1 Introduction

In his book on primate taxonomy, Groves (2001) changed the general view of *Lagothrix* taxonomy that had been established by Fooden (1963), as a wide-ranging species, with *L. lagothricha* being divided into four subspecies: *lagothricha, cana, poeppigii,* and *lugens.*

T. R. Defler (✉)
Departamento de Biología, Universidad Nacional de Colombia, Bogotá, Colombia
e-mail: thrdefler@unal.edu.co; thomasdefler@gmail.com

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Groves (2001) classified all the subspecies defined by Fooden as separate species, *L. cana, L. lagothricha, L. lugens,* and *L. poeppigii*, using as his argument for raising all subspecies to species that each taxon "is sharply distinct with no intermediates between them." In the same book, he argued for the use of a phylogenetic species concept for primates, such that a species is "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." According to him, this would underline the units of evolution existing in nature to a much greater degree than would the biological species concept (BSC) that until recently was the reigning species concept among biologists, at least when considering vertebrate animals (Groves 2001, 2004, 2012; Rylands and Mittermeier 2009; Rylands et al. 2000) and that the species would be testable, which they are not so easily under the BSC.

The arguments for using a phylogenetic species concept are that, at least in the Neotropics, a great deal of diversity is hidden and is being constantly discovered; the phylogenetic species underlines this great diversity yet to be described and the concept has been successful in pointing out many superspecies clusters (described for *Aotus* (distinguished by karyomorphs, Defler et al. 2001; Defler and Bueno 2007), *Callicebus* (hypothetically distinguished by phenotypes and more solidly by karyotypes, Defler 2010a, b), *Alouatta* (distinguished using molecular biology, Cortes-Ortiz et al. 2003), *Callithrix* (for genetics, see Rylands et al. 2000)). The disadvantage, according to other researchers, is that with this concept, more species would merit species status than traditionally recognized and the taxonomy of many groups would become unstabilized (Groves 2001, 2004, 2012; Isaac et al. 2004; Rosenberger 2012). Another criticism is that many subspecies have been automatically raised to species level without additional information about the particular species.

Fooden (1963) established the two Colombian *Lagothrix* taxa based on the holotype for *L. lugens*, collected by W. B. White from the Central Cordillera of the Andes and described by Elliot (1907). The description of *L. lagothricha* was made by von Humboldt and Bonpland (1812), based on a woolly monkey that was collected live from the Guaviare River near the mouth of the Amanavén River according to the collectors who sold the live monkey to von Humboldt in 1804 in the village of San Fernando de Atabapo on the Orinoco River.

Three recent genetic analyses (Ruiz-Garcia and Pinedo-Castro 2010, in press; Botero et al. 2010; Botero and Stevenson this volume) support a single species of *Lagothrix* in Colombia. But a recent morphometric analysis recognizes distinct phenotypes from the Eastern Cordillera in Colombia and distinguishes them as two new subspecies, from *lugens* of the Central Cordillera of the Andes (Mantilla-Meluk 2013).

This chapter discusses the many phenotypical differences within the Colombian *Lagothrix* and points out the lack of "sharply distinct" diagnostic characteristics between the taxa *lugens* and *lagothricha*, originally defined by Fooden (1963) as subspecies and later argued by Groves (2001) to be two separate species, *L. lugens* and *L. lagothricha*. This chapter suggests that *Lagothrix* in Colombia should be regarded as subspecies of *L. lagothricha* and that the two recently described subspecies need further study.

3.2 Methods

Collections Studied I studied all geo-referenced and non-geo-referenced *Lagothrix* museum skins from the main world collections of Colombian primates, listed as follows with their acronyms: the Instituto de Historia Natural of the National Colombian University (INC), Bogotá, Colombia; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAVH) of Villa de Leyva, Colombia; the Field Museum of Natural History (FMNH), Chicago, USA; the American Museum of Natural History (AMNH), New York City, USA; the United States National Museum (USNM), Washington, D.C., USA; and the Museum of Natural History (MNH formerly BMNH) of London, UK; and I noted descriptions of many live animals I have observed throughout the years. This analysis includes about 129 specimens of skins collected from Colombia and deposited in these collections.

Organization and Analysis of Specimens I mapped the 61 localities where these skins were collected or observations made. I geo-referenced the specimens that were previously listed on museum tickets and in museum catalogues using the described collection localities and employing best available Colombian maps and Google Earth to obtain best coordinates as well as mapping some of my own observations (Fig. 3.1). As a key to the mapped specimens, I include a gazetteer of these specimens in Appendix A (Table 3.1). I noted characteristics of most morphotypes and photographed the majority of them and I identified the location of all similar grouped morphotypes. Results were compared to Fooden's (1963) analysis, to Groves's (2001) revised taxonomy, and to Mantilla-Meluk's (2013) work, and I underline where my analysis differed from these authors. Figures for this chapter are available in color elsewhere on the Internet (http://www.thomasdefler.com/?page_id=220) and on the web page of Springer (www.springerimages.com). Each figure is indexed with a number in parenthesis that refers to the location of the specimen on the map (Fig. 3.1).

Photographing Specimens Digital photographs of museum specimens were usually captured by placing the head over a standardized gray field (Fig. 3.2), but I have not attempted to adjust tones of pelage color to the standard of gray tone that I used. Thus, caution is recommended when interpreting the pelage tones, since the gray field in each image may appear darker or lighter than the standard, showing that the pelage tones are actually lighter (in the case of a darkened gray field compared to the standard) or darker (in the case of a lighter gray field compared to the standard). After experimenting with flash and ambient light, I discovered that natural pelage color tones are best captured digitally using ambient light with no flash (Fig. 3.3a). Flash tended to emphasize reddish and yellowish tones to an exaggerated degree (Fig. 3.3b). Using ambient light resulted in many images being slightly darker than the tones perceived by the eye, perhaps due to the performance of the light meter when focused on the animal. The photography was accomplished using a Canon PowerShot S2 IS with a 12x optical zoom.

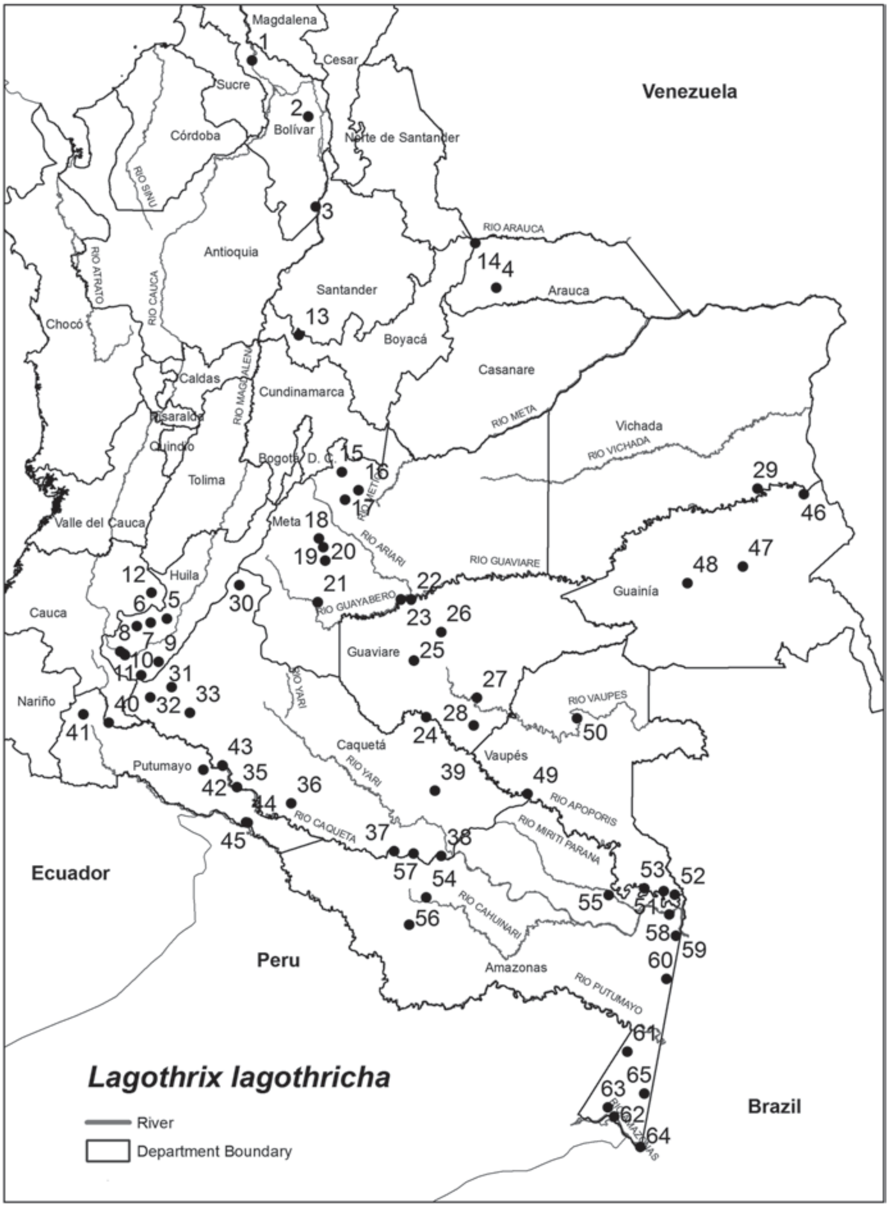

Fig. 3.1 Map of Lagothrix collecting sites and selected observations in Colombia

Table 3.1 Differences between *lugens* and *lagothricha*, sensu Fooden (1963)

Lagothrix l. lugens	*Lagothrix l. lagothricha*
Darker	Usually lighter but not always (Fig. 10)
Coronal stripe more common	Coronal stripe less common
Grizzled agouti arms, legs, body (not Central Cordillera)	Grizzled agouti arms, less common
Genetic differences Ruiz (26 specimens)	Gene (28 specimens)
230 polymorphic sites	37 polymorphic sites
15 haplotypes	14 haplotypes
Within the *L. lugens* clade there was one *L. lagothricha* detected	Within the *L. lagothricha* clade, there were two *L. lugens* individuals

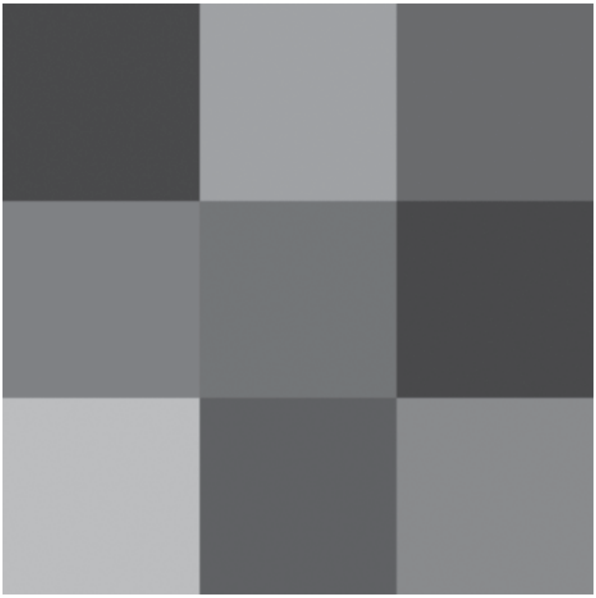

Fig. 3.2 Shades of gray (center square is standard in images). (From Wikipedia)

3.3 Results and Discussion

3.3.1 Descriptions of lugens

The holotype (MNH[BMNH] 1890.2.22.2) and paratype (MNH[BMNH] 1890.2.22.1) for *L. lugens* are deposited in the Natural History Museum, London, UK. They are both very dark (almost black) brown dorsally and ventrally (Fig. 3.3a, b, c, d). There are no lighter highlights nor are there beige- or cream-tipped hair or agouti (serially banded) forelimb and hindlimb hair that are common

Fig. 3.3 **a**. FMNH88474 Miraflores, Guaviare (not on map), photographed with ambient light; **b**. FMNH88475, Miraflores, Guaviare (not on map), photographed with camera flash; **c**. Holotype of *Lagothrix lugens*; photographed with flash (*left*) and ambient light (*right*) **d**. **e**. **& f**. Live *Lagothrix lugens* (3); numbers in parenthesis indicate the location on the map of specimens

from animals from the Eastern Cordillera. A live specimen (Fig. 3.3e, f) of this blackish *lugens* is illustrated from the region of Cantagallo, Bolivar, in the southern parts of Serranía de San Lucas, Bolivar. The typical uniformly dark brown (black) morphotype is found in all animals collected to date from the Cordillera Central de los Andes.

Confusingly, Elliot (1907) describes the entirely dark brown (blackish) holotype as follows, "Head, arms, and body dark purplish brown, almost black [up to here I completely agree]; legs and tail blackish brown washed with gray [the legs and tail are completely dark brown as the body], the hairs being blackish brown at the base, then black and tipped with gray or yellowish [this is not the holotype he is describing, which has no hairs tipped with gray or yellowish]; breast reddish chestnut [the breast is blackish, like the rest of the body]; rest of underparts black [I agree the underparts are black]." It is as if Elliot (1907) were describing an entirely different specimen. I have carefully examined the holotype for *L. lugens* twice, as well as the paratype, both of which I have photographed. I am astounded at Elliot's description, which in no way describes these two specimens, which can be seen in Fig. 3.3c, d. He obviously mixed up his notes here. However, his description partly fit specimens known for the Eastern Cordillera. For example, when he wrote this description, the London collection did have the specimens 1895.8.1.3 and 1895.8.1.4, which are *lugens* from the Eastern Cordillera and which fit some of the details of the description used by Elliot (1907).

Fooden (1963) included in the taxon *L. lagothricha lugens* not only the completely dark blackish *Lagothrix* known from the Central Cordillera but also the highly variable *Lagothrix* populations known from the Eastern Cordillera and the piedmont from the Caquetá River northward, even though these animals generally look different from the *lugens* holotype (except for some animals collected from the upper Caguán River, Caquetá, also with totally blackish pelage but additionally with white or beige-tipped hair not found in the Cordillera Central). The animals of the Eastern Cordillera are generally dark brown though not uniformly colored as is the holotype for *L. lugens*. They have many different tones of brown and gray and many have some sort of grizzled (gray or partly gray or brown) agouti or ticked bands of color that occur on each hair. The colors of these bands vary depending on the type of agouti coloration. Silver-tipped (brown or gray hair with guard hair that are tipped in cream or beige causing a silvery appearance) hair are also due to variable light colors. Many of these animals included in *lugens* by Fooden (1963) tend to have longer hair than many *lagothricha*, perhaps due to their living at higher elevations than most *L. l. lagothricha*. However, a *L. l. lagothricha* collected between the eastern Cordilleran creeks Rumiyaco and Rancheria from sub-Andean forest (generally identified as being at 1,000–1,800 m altitude) of Putumayo Department has longer hair than many *lugens* (Fig. 3.4a). Long hair is not generally considered to be a good mammalian diagnostic characteristic because of environmental (altitude, cold, etc.) effects.

Groves (2001) offers as a diagnosis for *L. lugens* "a variable taxon, but the overwhelming majority of specimens that I have seen are ticked [agouti] iron gray, with

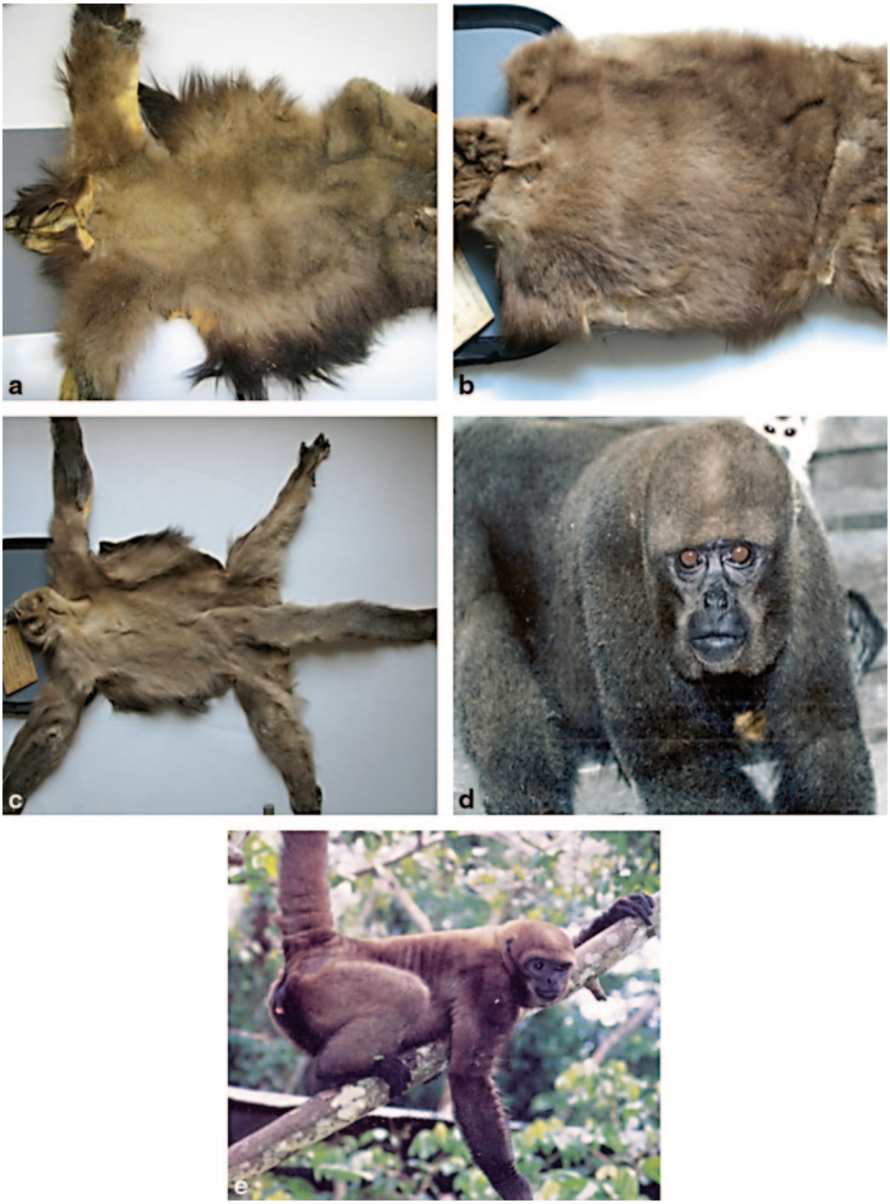

Fig. 3.4 **a**. IAVH6067, long-haired *Lagothrix lagothricha lagothricha* collected from premontane forest (1,000–1,800 m altitude) forest of the Cordillera Oriental (38); **b**. Light brown phenotype FMNH 89474 **c**. Miraflores, upper r. Vaupes, Miraflores, Guaviare (27); **d**. Nomi (well-known human-raised in the Amazon) from a population of *L. l. lagothricha* on the left bank Apaporis River, Vaupes, with light coronal stripe (53); **e**. Female from the Rio Pure, Brazil, without specific location and with light coronal stripe

somewhat blacker underside; hands, feet, tail, and anterior part of crown vary from slightly darker to black. Some specimens are brownish black all over [the holotype and paratype], with maroon [= dark brownish red, chestnut, fr. marron, Wikipedia] tones, and there is also a lighter, buffy gray morph with black restricted to the ventral midline except that the tail becomes black toward the end" (p. 192). This description includes, as does that of Fooden (1963), all of the dark animals from the Central and Eastern Cordillera, from the Arauca River and piedmont south to the Caquetá River, since he accepts Fooden's separation of taxa in Colombia.

3.3.2 Descriptions of lagothricha

In his revision of *Lagothrix*, Fooden (1963) defines *L. l. lagothricha* as "uniformly brownish on head and body, distributed north of the Rio Amazonas and east of the Rio Napo" (p. 213) and in the text of the same article "trunk pale brown; crown like back or paler" (p. 227). However, animals classified by Fooden (1963) as *lagothricha* include individuals similar to those described by von Humboldt and Bonpland (1812), but leave out populations of many other color phases or morphotypes as described below that are not only not "uniformly brownish on head and body" but may include other tones than "trunk pale brown"; such variants are not described by Fooden and vary from very light brown (Fig. 3.4b, c) to very dark brown (Fig. 3.4d) with many different highlights and even different textures of fur from loose and luxurious (Fig. 3.4a) to adpressed to the body (Fig. 3.4e).

Groves (2001) defines *L. lagothricha* as "Brown [all *Lagothrix* are some tone of brown] in color with ticking only on loins and tail or none at all [some *lagothricha* have agouti backs, many have agouti forearms]; head slightly paler [not always]; withers paler than shoulders [not always]: hands and feet grayer, darker [not always]; midline of underside jet black [not juveniles or young]" (p. 191).

The holotype for *Simia lagothricha* no longer exists, as the animal died during the difficult canoe travels of Humboldt and Bonpland on the Orinoco River and the skin was not preserved (von Humboldt and Bonpland 1812). Von Humboldt's type description is as follows:

"Son pelagees très moelleux, long, et uniforméte d' un gris de martre;" y

"SIMIA LAGOTHRICHA", imperbis, cinérea [= ash-colored], pilis apice nigrescentibus, facie atra, cauda prehensilis ubtus calva" both of which supposedly refer to an ash-gray color throughout the entire body [*uniforménte d'un gris de martre* or the Latin diagnosis *cinérea*]. Von Humboldt's description (diagnosis) of "pelage…long" is not uniformly true for *lagothricha* (Fig. 11). He also described the animal as being a uniform brown like the European hare, therefore "*lagothricha*" or "like hare pelage" and equally "like the gray of the martin", i.e., "d' un gris de martre" (p. 322; von Humboldt and Bonpland 1812). The colors described by von Humboldt do not approximate the colors of the European martin (*Martes martes, M.foina*); these animals are not colored gray as implied in his description, but rather vary from light to dark brown (Fig. 3.5a, b), closer in color to that shown in Fig. 3.4d, the darkest brown Amazonian population so far reported for *L. lagothricha*, while calling this primate *L. lagothricha* as being hare colored suggests the color illustrated in Fig. 3.5c, showing a European hare (*Lepus europeus*), much lighter than all specimens seen by this author and in the author's experience agreeing with few *L. l. lagothricha*, but vaguely with the anomalous Fig. 3.4a, a supposed (according to Fooden 1963 and Hernández and Cooper 1976) *L. l. lagothricha* from the Eastern Cordillera at sub-Andean altitudes of between 1,000 and 1,800 m.

Von Humboldt's taxon has been commonly called "Humboldt's Woolly Monkey" and it may be most closely illustrated by Fig. 3.4e, from the Puré River of Brazil and Colombia, which has an overall similar tone and illustrates a very commonly observed phenotype in the Colombian Amazon that is a light brown (but not similar in color to either the European hare or the European martin). A specimen collected by this author (IAVH6037; Fig. 3.5d) while working for the former government environmental agency INDERENA from the fluvial island south of the lower Amanavén River (also called the Río Uva) in Vichada (bordered on the south by the Guaviare River and not far from the putative type locality) may also be a similar color, although the color pattern does not agree with von Humboldt's basically unicolor description of the holotype. In the case of Figs. 3.4a and 3.5c, the head and neck are lighter brown, contrasting with the back (a characteristic included for the taxon by Fooden 1963; and not seen in *lugens*).

What are we to make of all this? Von Humboldt's description (during this phase of the writing, Bonpland hardly contributed at all) of *Simia lagothricha* is not encouraging. We know that the specimen was the same tone of brown (or gray) both dorsally and ventrally (contra Fig. 3.5d, the specimen collected closest to the mouth of the Amanaven River but similar to either Fig. 3.4d from the Apaporis River or Fig. 3.4e from the Puré River). To summarize, the three contrasting designations used by von Humboldt to characterize the color of his holotype were a dark brown (like the martin), a lighter brown (like the European hare), and an ash-gray (which is not a common color seen in the Colombian Amazon, but which apparently exists south of the Putumayo River in Peru and Ecuador; see Fig. 3.5d). This does not inspire confidence that *L. l. lagothricha* has been well defined as either a subspecies (as in Fooden 1963) or a phylogenetic species, *L. lagothricha* (sensu Groves 2001).

In the case of calling *L. lagothricha* "light brown," it is true that most of the animals from the eastern Amazonian silvatic plains seen by this author are lighter brown than are the Eastern Cordillera animals. However, Fig. 3.4d clearly illustrates a *lagothricha* morphotype that is dark brown and, according to the Makuna Indians who hunted this specimen's mother, the local population is the same dark brown color. Also, Fig. 3.5d illustrates a gray *L. lagothricha* collected and without notes along the Putumayo River (probably from the south bank, as known specimens from the north bank are totally different), so calling *L. l. lagothricha* "light brown" is not diagnostic because of dark brown and gray animals. The animal in Fig. 3.5e collected from an unknown location by Watanabe in Puerto Leguízamo,

Fig. 3.5 **a**. European martin; **b**. European hare; **c**. IAVH 6063, *L. l. lagothricha* from Amanaven River, s. Vichada (not far from type locality at the mouth of the Amanven River into the Guaviare River) (29); **d**. From somewhere on the lower Caquetá River. (45); **e**. IAVH 2695 near Puerto Leguizamo, Putumayo (45); This *lagothricha* has grizzled forearms like many *lugens* and a very light coronal stripe; **f**. animal from the lower Apaporis River (53)

Fig. 3.6 **a**. IAVH 2628 *L. lagothricha* south of Guaviare River with slight agouti on lower back and shoulders (22); **b**. *L. lagothricha* from somewhere on the lower Caquetá River, according to Yucuna Indians who had hunted this specimen's mother. She has a clear coronal stripe. This specimen's forearms are also grizzled; **c**. FMNH 33889 *lugens* Bojaba, Boyacá (14); **d**. FMNH 92333 *lugens* Bojabá, Boyacá (14); **e**. FMNH 70601, *lugens*, Consaya River, Caquetá (31); **f**. FMNH 70602 *lugens* Consaya River, Caquetá (31)

Putumayo, was noted in the catalogue. But Watanabe had traveled to the Penilla River (*L. l. lugens* sensu Fooden 1963; Hernández Camacho and Cooper 1976) and also had been collecting in the region of Puerto Leguízamo, Putumayo (*L. l. lagothricha* sensu Fooden 1963; Hernández Camacho and Cooper 1976); but the specimen (IAVH2695) does not conform to other specimens specifically collected in the Penilla Creek region (IAVH1616, IAVH1617, map no. 33) as *L. l. lugens*, nor does it resemble other specimens of *L. l. lagothricha* collected close to Puerto Leguízamo (for example, IAVH0599 map no. 41) and it exhibits other (besides the color) characteristics (i.e., head and back lighter than back and sides) that have been used as a diagnosis for *L. l. lagothricha* and have led to its diagnosis as such.

Groves (2001) defines *L. lagothricha* as having "ticking (agouti) only on the loins or tail or none at all," yet I have seen many specimens with agouti forearms (Fig. 3.5e), and sometimes the back shows ticking (Fig. 3.6a), like some specimens from the Eastern Cordillera. Fooden (1963) stated that coronal stripes are limited to his *lugens*, yet occasionally coronal stripes are seen on *lagothricha* as well (for example Fig. 3.6b; an unrecorded local site on the lower Caquetá River).

In many museum specimens, the crown of the head is often obscured by the folded head skin so that the characteristics of the head are not clear. It was only from being familiar with several live specimens from the Colombian Amazon that it became clear to me that some specimens do exhibit a coronal stripe, similar to *lugens*, although the incidence of the coronal stripe is not as common in *lagothricha* as it is in *lugens*, and because of the lighter brown tones in *lagothricha*, the stripe is not as clear as in the darker *lugens*.

Fooden's (1963) definitions of *lugens* and *lagothricha* on which Groves (2001) partly bases his phylogenetic species *L. lugens* and *L. lagothricha* are confusing; the definition of *lugens* includes not only the confusingly defined holotype but also includes the animals with many gradations toward *lagothricha*. He describes *lugens* as "trunk pale silver-gray to dark brown or blackish; with or without contrastingly dark crown patch; pale mid-sagittal coronal streak frequently present". Yet, many of these characteristics (i.e., trunk silver-gray to dark brown or blackish; pale mid-sagittal coronal strip) are sometimes found in Fooden's *lagothricha* as well. He describes *lagothricha* as "trunk pale brown; crown like back or paler," true for some *lagothricha*, not so for others. These descriptions have proven to be inadequate for the identification of many Colombian *Lagothrix*, which are actually much more variable than suggested above and which seem to me to intergrade with each other in the manner of the modern concept of subspecies (Wilson and Brown 1953; Mallet 2007). That is to say, there are no sharp boundaries between *L. lugens* populations of the Eastern Cordillera and piedmont forests with populations usually recognized as *L. lagothricha*. It seems that a useable diagnosis for the species *L. lagothricha* (sensu Fooden 1963; Groves 2001) does not exist except for a strict definition of *lugens* only from the Central Cordillera to Cueva de los Guácharos National Park (no. 9 in Fig. 3.1).

From my study of the Colombian *Lagothrix*, I would define *lugens* as "trunk dark brown (blackish) with no contrasting crown, dorsum or tail; the same color throughout the body, limbs and tail," thus confining *lugens* to the Central Cordillera extending from the Serrania de San Lucas in the north to the Cueva de los Guacharos National Park. I would define *lagothricha* (sensu Fooden 1963) as trunk pale brown to dark brown (blackish) and sometimes grayish; coronal streak occasionally present (similar to many *lugens*) but mostly absent; sometimes with forearms and lower legs with agouti contrasting with lighter body color (similar to many *lugens* of the Eastern Cordillera); texture of fur varying from very short, tightly adpressed (i.e., lying flat against the body as shown in Fig. 11) to body to long, loose (example Fig. 3.4d; similar to many *lugens*).

I contend in this paper that the Colombian *Lagothrix* taxa as defined by Fooden (1963) and Groves (2001) are not sharply distinct and that they in fact consist of a mosaic of phenotypes that arguably do not permit an orderly division between *lugens* and *lagothricha*, such that separating them as either species or subspecies does not reflect two distinct phenotypes that could potentially be units of evolution.

The conversion of subspecies into species without further analysis is problematic, especially when there are poorly described subspecies that are actually very difficult or impossible to distinguish and on this basis, phylogenetic species are declared. Upgrading subspecies to species level should only be done when accompanied by reexamination of available evidence (pers. com. Colin Groves). This is the problem of *lugens* and *lagothricha*. However, upgrading subspecies of *Callicebus torquatus* is also a problem (Van Roosmalen et al. 2002). Two taxa (subspecies) of *C. torquatus* (sensu Hershkovitz 1990), *lugens* and *lucifer*, are not distinguishable by phenotype (despite Hershkovitz's 1990 key). In these two cases, however, the taxa are distinguishable by karyotype, but different taxonomic interpretations are required with this information. *C. lugens* is clearly appropriate because of its distinctive chromosome number, but new karyotypic information and distributions of the three subspecies, *torquatus, lucifer, and medemi*, indicate that these belong to one species with three subspecies (Defler 2010a, b; Hershkovitz 1990) instead of three species.

Recently, Mantilla-Meluk (2013) described two new subspecies of what he called *L. lugens* from the Eastern Cordillera referring to *lugens* (sensu Fooden 1963). Each population was collected from the eastern lowlands: *L. l. sapiens* corresponds to a series collected by Hershkovitz at around 500 m (no. 43 in Fig. 3.1), and *L. l. defleri* is from the piedmont of the Serrania de La Macarena (500–1,000 m; nos. 18–20 in Fig. 3.1) and possibly higher elevations (not registered in the catalogue or on the specimen tickets) that were included in the extensive collection by Dillon in the 1941 American Natural History Museum expedition (Gilliard (1942) and others, such as von Sneidern from Los Micos and Yerly Creek. This research is based on morphometric skull measurements and phenotypic differences and accepts the bi-specific *Lagothrix* for Colombia proposed by Groves (2001).

Whether these newly defined subspecies adequately describe the total variation observed from the Eastern Cordillera to the eastern piedmont is equivocal. Eastern Cordilleran populations defined by Fooden (1963) as *lugens* range from close to the Arauca River border with Venezuela (Bojabá, Boyacá, Fig. 3.7a, b and no. 14 in Fig. 3.1) in the north to the Caquetá River in the south and east to the Ariari River (above the Guaviare River) and to the Yari River (below the Guaviare River), a considerable distance from the Cordillera. *L. l. sapiens* (Mantilla-Meluk 2013) described from the Consaya River in southern Caquetá corresponds to Fig. 3.7c, d in this chapter, and *L. l.defleri* (Mantilla-Meluk 2013) described from the Sierra La Macarena corresponds to Fig. 3.7e, f.

Mantilla-Meluk (2013) uses morphometric and phenotypic data for his analysis, finding some clear morphometric differences among the three populations of *lugens*. He defines the external phenotype for what he calls *L. l. sapiens* as "overall silver coat color and a black cap ornate with a gray or silver mid-sagittal coronal stripe," and that of his *L. l. defleri* as "a darker coloration in comparison with *L. lugens* from the Amazon; less defined cap and mid-sagittal stripe; a larger body size compared to *L. l. lugens* [*sensu* Mantilla-Meluk 2013] from the highlands; a shorter tail than *L. lugens* [sensu Groves 2001] from the Amazon (i.e. *L. l. sapiens;* longer hair than in *L. lugens* [sensu Groves 2001] from the Amazon." Nevertheless, Mantilla-Meluk (2013) chose a series of skins from the Aguas Claras Creek, San Antonio, to represent *L. l. lugens* (Fig. 3.8a, b), which would include all the *L. lugens* from the Central Cordillera, but these, although are generally dark brown (blackish) throughout their body, have a slight ticking of gray on their flanks and tail, something not apparent in the holotype and paratype and those examples that I have seen throughout the Central Cordillera. These *Lagothrix* are reminiscent of the northernmost collected animals from Bojabá, Boyacá (Fig. 3.7a, b), although those from northern Boyacá are more heavily "silvered" throughout.

Fig. 3.7 **a**. FMNH 33889, *lugens*, Bojaba, Boyacá (14) (19); **b**. FMNH 92333, *lugens*, Bojabá, Boyacá (14); **c**. FMNH 70601, *lugens*, Consaya, Caqueta (31); **d**. FMNH 70602, *lugens*, Consaya River, Caquetá (31); **e**. FMNH 87775, *lugens*, La Macarena, Yerly creek (19); **f**. AMNH142236, *lugens*, La Macarena, Meta (19)

Fig. 3.8 **a**. FMNH 70586, *lugens*, San Adolfo, Aguas Claras, Huila (9); **b**. FMNH70576, *lugens*, Acevedo, Aguas Claras, Huila (9); **c**. Young male *lugens* from the Eastern Cordillera. He was confiscated by government authorities on the Florencia-Neiva road. This individual does not fit into pelage descriptions for *sapiens* or *defleri*; **d**. IAVH 1615, *lugens*, Puerto Japon, Peneya River, right bank; this does not exhibit a phenotype for *sapiens* (32); **e**. IAVH 6062, *lugens*, Police Inspection Station, Guayabal, Caqueta (26); **f**. FMNH 88245 Trapiche, Guaviare River, Guaviare (23)

Apart from the morphometric data that distinguish these three populations, many other phenotypes of *Lagothrix* along the Eastern Cordillera do not seem to fit into any of these three defined taxa. These phenotypes easily might belong to small populations, but information about this is unavailable until additional field studies are made. A woolly monkey confiscated along the road between Florencia, Caquetá, and Neiva, Huila (Fig. 3.8c), has a blackish head and grayish body (i.e., gray fur tipped with white or beige, simulating a grayish tone). Animals collected along Peneya, Creek, Caquetá (only about 30–40 km west of the locality for the described *Lagothrix l. sapiens* and with no fluvial barriers and within the distribution defined for this taxon), are markedly more brownish with shorter hair and a black mid-dorsal stripe (Fig. 3.8d). There are many other examples that do not agree with any of Mantilla-Maluk's defined "*lugens*" taxon. It would be interesting to know how these non-conforming phenotypes (i.e., neither falling into the two new taxa, nor into the nominotypical *L.l.lugens*) might fit morphometrically into this new scheme. Mantilla-Maluk's subspecies essentially seem to describe three small populations, perhaps micro-geographic races and given the high phenotypic diversity of *L. lagothricha* it is perhaps reasonable to ask whether assigning a trinomial to these populations is useful, especially since information in this chapter and elsewhere suggests that all *L. lagothricha* in Colombia correspond to one highly polymorphic species. However, analysis and description of the genetic and phenotypic diversity within *L. lagothricha* is certainly useful.

3.3.3 Subspecies Converted ad hoc to Species

I question whether subspecies (especially poorly described subspecies) in many cases can be equated to "units of evolution" ("No arbitrary criterion is available to define the category subspecies, nor is the subspecies a unit of evolution except where it happens to coincide with a geographic or other genetic isolate." Mayr and Ashlock 1991); being a unit of evolution is one of the justifications for the use of the phylogenetic species concept in the first place. More modern analyses have found that, indeed, many populations currently classified as subspecies do exhibit differences at morphological, behavioral, and genetic levels (Mallet 2007) that could define in some way a significant unit of evolution (ESU; Moritz 1994; Davis and Nixon 1992), but many do not. Indeed, it seems to me that the concept of subspecies has evolved in the literature to mean more than it was originally intended to (i.e., "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species." Mayr and Ashlock 1991). Ironically, strict users of the phylogenetic species concept (Cracraft 1983, 1992) and some users of the BSC (Wilson and Brown 1953) criticize the use of subspecies (but for different reasons).

The original concept of subspecies was meant to be shorthand for an allopatric taxonomic unit for an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species. A subspecies is characterized as (1) a collective category, (2) named if there are sufficient diagnostic characters, and (3) its assignment to subspecies often involves overlap of the ranges of variation (Mayr 1963; Mayr and Ashlock 1991). Subspecies are not necessarily evolutionary units in contrast to the "modern" view where a subspecies has become not only an evolutionary unit, but has come to be identified also via their genome, a problematic inflation of the term subspecies that deserves to be analyzed, discussed and criticized.

3.3.4 What is an Adequate Taxonomy for Lagothrix in Colombia?

Had I revised *Lagothrix*, I would not have grouped animals from the Central Cordillera that correspond to the holotype of *lugens* with animals of the Eastern Cordillera, which to me seem quite different from the black animals originally called *lugens* by Elliott (1907) and that can be diagnostically defined from the Eastern Cordillera. It seems clear to me that the holotype for *lugens* is a completely dark-brown (blackish) animal with no highlights of other brown tones and no agouti coloration or silver-tipped hair that typically are found in animals from the Eastern Cordillera. It is important to underline that in Elliot's original description of *L. lugens*, although he assigns specimen number B.M. 90.2.22.2 as the type specimen, his description of the phenotype seems to be based on some other specimen. This certainly complicates my argument.

The Eastern Cordillera phenotypes are variably colored brownish or grayish animals often with grizzled forearms and contrasting tones on the tails, back, and flanks, sometimes with coronal stripes that Fooden uses as diagnostic characters to distinguish these from *lagothricha* (some of which also show coronal stripes) and often with a "silvery" gray appearance ("silvery" being some hair tips ending in cream or beige that intercalated among gray pelage hair gives a silvery appearance), also similar to at least one Amazonian population of *L. lagothricha* (Fig. 3.5e). Central Cordilleran *lugens* have none of these characteristics. Two specimens (Fig. 3.8e) collected from the upper Caguan River are the only specimens from the Eastern Cordillera that I have seen that seem to be of a uniformly dark brownish (blackish) color both dorsally and ventrally (although the heads are missing) like Central Cordilleran *lugens*, but these two specimens show silvering (cream-tipped guard hair) over the entire dorsum, unlike true Central Cordilleran *lugens*.

The definition of *lugens* as "trunk pale silver-gray to dark brown or blackish; with or without contrastingly dark crown patch; pale mid-sagittal coronal streak frequently present" (Fooden 1963) certainly describes a wide variety of phenotypes, even more so than his diagnosis of *lagothricha* as "trunk pale brown; crown like back or paler" which is more restricted in definition. Yet, *lagothricha* seems as variable as *lugens* and populations have trunks varying from pale brown to blackish brown to silvery gray (Figs. 3.4a, d, 3.5e). A *lagothricha* specimen from the Guaviare River (Guaviare; Fig. 39) is silvery agouti gray throughout the body and limbs. Certainly, *lagothricha* phenotypes are as variable as are *lugens* phenotypes and exhibit many characters in common and cannot be called distinct from each other.

Three Colombian genetic analyses support my conclusion that only one *Lagothrix* species exists in Colombia, *L. lagothricha* (Ruiz-Garcia and Pineda-Castro 2010, in press; Botero et al. 2010; Botero and Stevenson this volume). Ruiz-Garcia and Pineda-Castro (2010) analyzed the mitochondrial COII gene from 97 georeferenced *Lagothrix* specimens obtained in the field and representing the four taxa described by Fooden (1963; including 26 *lugens* and 28 *lagothricha*). They found *lugens* to be genetically the most diverse taxon (followed by *poeppigii*), while the least diverse taxa were *lagothricha* and *cana*. Two evolutionary lineages were detected within the *lugens* and the major *lagothricha* haplotype was shared with *lugens* and the genetic distances from the major part of the *lugens* haplotypes when compared to *lagothricha* were very low and comparable to subspecies defined in *Ateles* (Collins and Dubach 2000, 2001). Ruiz-Garcia and Pineda-Castro (2010, in press) concluded that all the *Lagothrix* haplotypes belonged to the same species, i.e., *L. lagothricha*. Very striking was the discovery of *lugens* genotypes within the accepted range of *lagothricha* and some *lagothricha* genotypes within the recognized range of *lugens*.

Botero et al. (2010) sampled blood from 16 captive *Lagothrix* whose geographic origin was unknown. Taxa were identified in this study by phenotype and traditional separation between the two taxa (Hernández-Comacho and Cooper 1976; Fooden 1963; Defler 2010a, b). Karyotypes were determined and the mitochondrial COII gene and mitochondrial D-loop were amplified for analysis. There was high karyotypic variability, especially in chromosomes 4, 7, and 24, and these variants were observed across the taxa, suggesting subspecific designation instead of specific. In the molecular analysis, six haplotypes were found for *lagothricha* and nine for *lugens*. Although nuclear diversity was higher in *lagothricha*, no significant differences were found between the taxa in phylogenetic trees obtained by three different methods.

Botero and Stevenson (this volume) used mitochondrial DNA sequences to study gene flow between the populations of Colombian *Lagothrix*. They found high rates of gene flow between adjacent populations of the two taxa (determined by coat color) found in Guaviare (*lagothricha*) and Meta (*lugens*) that is not consistent with a two-species view as distinguished by coat color and distribution.

Whether these conclusions affect the taxonomic status of *L. poepiggii* and *L. cana* is an obvious question. Although these taxa seem to be more clearly distinct from one another than *lugens* and *lagothricha*, genetic evidence suggests that these may also best be considered as subspecies of *L. lagothrica* (Ruiz-Garcia and Pinedo-Castro 2010, in press).

3.4 Conclusion

Lagothrix phenotypes in Colombia do not define taxa previously described for the country.

1. The only coherent taxon of *Lagothrix* for Colombia is *lugens*, defined as only those *Lagothrix* from the Central Cordillera of the Andes and which are identical to the holotype and paratype.
2. Populations of *lugens* (sensu Fooden 1963) from the Eastern Cordillera and piedmont of the Andes have not truly been diagnostically defined, sharing as they do some of their defined characters with *lagothricha* (sensu Fooden 1963). These taxa are not "sharply distinct" as sustained by Groves (2001).
3. Sharing of characters used before as diagnostic for one taxon (*lugens* of the Eastern Cordillera and piedmont) with the other taxon (*lagothricha* sensu Fooden 1963) suggests a taxonomic level of subspecies rather than species.
4. Recent splitting of the previously classified taxon *lugens* of the Eastern Cordillera and piedmont of the Andes into two new taxa, *sapiens* and *defleri* (but as subspecies of *L. lugens*, not *L. lagothricha*), seems problematic, since it is not clear whether these two subspecies include other *Lagothrix* populations of the Eastern Cordillera and piedmont of the Andes or whether they represent micropopulations. Craniometry and phenotype analysis of specimens from throughout the Colombian range of woolly monkeys is needed to test the validity of these two new taxa.
5. Recent genetically based research on Colombian *Lagothrix* supports the concept of one *Lagothrix* species for Colombia, *L. lagothrix*, which might be divided into at least four subspecies, although subspecies designations require more analysis (see (3) above) and the most logical diagnosis is that *lugens* is generally a darker taxon than *lagothricha*.
6. High phenotypic diversity of *L. l. lagothricha* and *L. l. lugens* is distributed in a mosaic of populations with no recognized clines.

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Gazetteer for *Lagothrix lagothricha*

Lagothrix lagothricha

Bolívar

1. Maganqué, [9°13′32.85″N, 74°43′58.39″], ND, ND, IAVH0760
2. Serranía de San Lucas, Norosí, captive in La Fiebre farm, [8°31′49.33″N, 74°02′13.05″W], col. K. Green, 06/16/1972, IAVH1505; col. H. Chiriví & R. W. Cooper, 16/06/1972, IAVH1607
3. During walk between Puerto Argelia- Esperanza- Floresta in mcpio Cantagallo [extreme s. Bolívar] [7°25′04.17″N, 73°56′47.44″W], obs. Carlos Zamora Arrienta, (fotos available of young animal)

Arauca

4. Tame, forests around Fortul, [6°25′N, 71°43′W], col. G. Romero, 26/03/1972, ICN6892

Huila

5. "Tolima Mountains" [now Huila], 2°20′N, [75°47′29.27″W], col. R. B. White, 22/02/1890, NHM(BMNH)1890.2.22.1, NHM(BMNH)1890.2.22.2 [holotype *Lagothrix lugens*][I placed the collection site at about 1,900 m on the east slope of the Cordillera Central]
6. R. Moscopán, [2°16′59.25″N, 75°58′58.88″W], col. K. von Sneidern, 05/1937, FMNH84550
7. Popayan, Moscopán, [2°14′32.64″N, 76°09′20.44″W], col. J. Wallis, n.d., AMNH149263, AMNH149265
8. La Palma, [1°55′30.70″N, 76°21′39.46″W], col. L. E. Miller, 28/04/1912, AMNH33889, AMNH33890, AMNH33891, AMNH33892, AMNH33893, AMNH119249
9. Acevedo, r. Aguas Claras, San Adolfo, 1°48′N, 75°53′W [1°39′53.5″N, 76°00′52.17″W], col. P. Hershkovitz, 14–29/06/1951, FMNH70574, FMNH70575, FMNH70576, FMNH70577, FMNH70578, FMNH70579, FMNH70580, FMNH70581; 20–27/08/1951, FMNH70582,
10. San Agustín, San Antonio, 1°53′N, 76°18′W, col. P. Hershkovitz, 23/08/1951, FMNH70583; 27/08/1951, FMNH70584, FMNH70585, FMNH70586; 04/09/1951, FMNH70587, FMNH70588, FMNH70589
11. Mcpio Acevedo, Guácharos National Park, La Argelia, [1°38′00.91″N, 76°06′03.75″W], col. P. Hershkovitz, IAVH0240

Cauca

12. Paez, [2°39′02.54″N, 75°58′27.05″W], col. H. Le Nestour, ND, ICN192

Boyaca

13. El Cobre [creek.?], Chala, [5°49′44.93″N, 74°09′23.28″W], co. NB, 17/06/1895, MNH(BMNH)1895.8.1.3, MNH(BMNH)1895.8.1.4

14. Bojabá, [r. Bojabá], [6°58′3.55″N, 71°58′35.96″W], col. K. von Sneidern, 18–25/03/1959, FMNH92331, FMNH92332, FMNH92333, FMNH92334, FMNH92335

Meta

15. Villavicencio, [4°08′20.53″N, 73°37′21.05″W], col. N. Miller, 01/01/1923, AMNH63933. AMNH63934
16. Villavicencio, vda Tarané, forest between c. Suría and r. Negro, Hda. San Antonio, [3°55′N, 73°25′W], col. J. Hernández-C., C. Velazquez, 21/08/1955, ICN102, ICN163, ICN1543, ICN1777
17. San Martín, r. Guamal, [3°48′01.8″N, 73°34′57.49″W], col. F. C. Lehman, 14/03/1958, FMNH89490, FMNH89491, FMNH89492, FMNH89493
18. San Juan de Arama, Los Micos, [3°19′08.18″N, 73°54′22.10″W], col. K. von Sneidern, 28 April 1957, FMNH87782
19. La Macarena, r. Yerly, [3°12′50.92″N, 73°51′09.29″W], col. K. von Sneidern, 24/02/1957, FMNH8775, FMNH8776, FMNH8777; 10/03/1957, FMNH8778, FMNH8779, FMNH8780. FMNH8781
20. Sierra La Macarena [American Museum expedition], [3°02′38.96"N, 73°49′42.48"W], col. J. Dillon, 04–05/05/1942, AMNH142234, AMNH142235, AMNH142236, AMNH142238, AMNH142239
21. R. Duda, left bank, cabaña INDERENA, [2°31′57.94″N,73°55′20.69″W], col. T. O. Lemke, 24/11/1975, IAVH2845

Guaviare

22. R. Ariari, right bank of r. Guaviare at mouth of R. Ariari, [2°34′11.45″N, 72°46′04.03W], col. J. Morales, C. Chaparro, 11/11/1977, IAVH2585, IAVH2593, IAVH2628
23. Upper r. Guaviare, El Trapiche narrows, west, [2°34′08.81″N, 72°53′37.94″W],?????
24. Left bank r. Apaporis, La Providencia [Puerto Yaviya], [1°06′57.77″N, 72°34′55.38″W, col. F. Medem, 5/03/1952, ICN1755 [map in Medem (1981)]
25. Trueno Creek, 30 km SW of San José, [ ], col. F. Medem, 23/01/1957, FMNH88242
26. Barracón, R. Itilla, [ ], col. F. Medem, 13/02/1958, FMNH89473
27. Miraflores Creek, [ ], col. F. Medem, 22/03/1958, FMNH89474, FMNH89475, FMNH89476, FMNH89477
28. Upper Tucunemita Creek, Campo Grito, [1º00′58.60″N, 71º59′45.95″W], col. F. Medem, 31/12/1957, FMNH89472

Vichada

29. R. Uva, right bank, [3°56′08.55″N, 68°29′35″W], col. T. R. Defler, 16/04/1984, IAVH6037

Caquetá

30. San Vicente de Caguan, police inpection station, Guayabal, Andalucia farm, 2°44′41″N, 74°53′22″W, col. Y. Muñoz, 12/1997, IAVH6061, IAVH6062

31. La Morelia, [1°29′13.72″N, 75°43′32.28″W], col. L. E. Miller, 01/07/1912, AMNH33651, AMNH33652
32. San José de Fragua, vda La Esmeralda, r. Yurayaco, National Park Altofragua-Indiwasi, [1°21′40.12″N, 75°59′18.01″W], col. F. Quevedo, 9/09/2000, IAVH6772
33. Milan, La Rastra. R. Orteguaza, [1°10′04.84″N, 75°29′59″W], col. S. Trisler, 06/1935, AMNH129402, AMNH129403
34. R. Consaya [left bank r. Caquetá], [0°30′54.66″N, 75°05′41.84″W], col. P. Hershkovitz, FMNH70601, FMNH70602, FMNH70603, FMNH70604, FMNH70605
35. R. Caquetá, left bank, below Puerto Boy,[0°15′14.05″N, 74°55′03.31″W], col. H. Granados, H. Arévalo, 05/01/1960, ICN079 [listed as "Putumayo", but "left bank" puts it in Caquetá; these collectors made many mistakes in their notes, should be interpreted with precaution]
36. R. Peneya, Puerto Tokio, right bank, [0°02′58″N, 74°15′W], col. K. Izawa, 12/1971, IAVH1615
37. Cuemani, bank of r. Caquetá, Cuemaní community, [0°32′16.66″S, 72°58′39.18″W], col. W. Townsend, 19/12/1984, IAVH5250
38. Araracuara, left bank r. Caquetá, [0°35′57.42″S, 72°23′55.34″W], col. R. Franco, 10/1984, IAVH4244, IAVH5244; col. W. Townsend, 1983, IAVH5303; col. E. Barriga, 04/1965, ICN1548
39. Above the rapids of r. Yari [one assumes the lowest rapids on the Yarí, since there are many, but the lower rapids are the most accessible], [0°12′30.47″N, 72°28′34.95″W], col. J. Sanchez, 06/1972, IAVH1618

Putumayo

40. Mpio Mocoa, Puerto Limón, Serranía de los Churumbelos, camino Indiyacu-Mocoa [1°03′00.46″N, 76°30′0.86″W], col. C. O. León, J. Fuentes, E. Chaparro, 27/05/1972, ICN14775
41. Putumayo-Nariño, upper drainage Rumiyaco-Ranchería rivers (Kofan territory), [1°09′10″N, 76°48′46.24″W ESTIMATED], col. Y. Muñoz, 11/09/1998, IAVH6067, IAVH6068, IAVH6069
42. R. Mecaya, [0°27′59.81″N, 75°19′59.9″W], col. P. Hershkovitz, 02–23/03/1952, FMNH70590, FMNH70591, FMNH70592, FMNH70593, FMNH70594, FMNH70595, FMNH70596, FMNH70597, FMNH70598, FMNH70599, FMNH70560,
43. R. Consaya, [0°31′09″N, 75°05′49.96″W], col. P. Hershkovitz, 18–25/03/1952, FMNH0561, FMNH0562, FMNH0563, FMNH70564, FMNH70565
44. Puerto Leguizamo, Caucayá C. Velasquez farm, Limoncocha, [0°10′55.28″S, 74°48′27.69″W], col. H. Chiriví, J. A. Mora, 01/08/1973, IAVH0599
45. Puerto Leguizamo, [0°11′16.66″S, 74°47′08.69″W], col. Watanabe, 1973–1974, IAVH2695

Guainía

46. Puerto Inírida, [3°51′54.85″N, 67°55′25.58″W], col. W. Townsend, 27/02/1981, IAVH5596

47. Puerto Inírida, Morroco community rapids, [2°58′30.72″N, 68°40′22.31″W], col. W. Townsend, 13/04/1981, IAVH6089, IAVH5583
48. R. Inírida, c. Zancudo, [2°46′10.83″N, 69°21′26.78″W], col. W. Townsend, 19/04/1981, IAVH5595

Vaupés

49. R. Pacoa, [0°10′N, 71°20′W], col. F. Medem, 02/1912, ICN2174, ICN4714, ICN4715
50. [Left bank r. Vaupés], Mandí, [1°06′00.29″N, 70°43′11.23″W], col. J. Morales, C. Cruz, A. Samper, 09/11/1973, IAVH1547
51. R. Apaporis, left bank c. Pintadillo, 1°02′S, 69°39′W, obs. E. Palacios, 2001–2003, [Palacios & Peres, 2005]
52. Estación Biológica Mosiro Itajura-Caparú, [1°04′32.8″S, 69°30′55.47″W], obs. T. R. Defler (1995, 1996, 1999)
53. Nomi Wolly Monkey 1º0′3.79″S 69º53′21.6″W, black woolly taken by indigenous locals, raised by humans

Amazonas

54. R. Apaporis, La Providencia (Yaviya), [1°06′42.08″N, 72°34′54.89″W], col. F. Medem, 10/02/1952, ICN1797
55. R. Mirití-Paraná, Puerto Rastrojo, right bank, [1°05′S, 70°20′W], col. T. R. Defler, 12/08/1980, IAVH3025, IAVH3031, IAVH5990
56. La Chorrera, [1°26′54.39″S, 72°47′32.47″W], col. W. Townsend, 12/1984, IAVH5246
57. R. Caquetá, left bank, Cachaní rapids, [0°34′01.50″S, 72°44′28.72″W], col. T. R. Defler, 04/1993, IAVH6019
58. R. Caquetá, La Pedrera, [1°19′24.29″S, 69°34′58.29″W], col. E. del Giudice, 12/08/1987, IAVH5590, IAVH5591, IAVH5592
59. R. Caquetá, right bank, c. El Ayo, 1°35′S, 69°30′W, obs. E. Palacios, 2001–2003, [Palacios & Peres, 2005]
60. R. Puré, right bank, [2°07′09.98″S, 69°37¨W], obs. T. R. Defler,
61. R. Cotuhué, left bank, Santa Rita, [3°01′S, 70°06′W], col. T. R. Defler, 04/1993, IAVH6030, IAVH6034
62. Amacayacu National Park [administrative center], [3°49′05.02″S, 70°15′45.71″W], col. A. Villa-L., nd, IAVH5337, IAVH5738; col. C. Campos, nd, IAVH5366
63. R. Amacayacu, c. Brava, [3°42′13.23″S, 70°20′21.21″W], col. J.Sinisterra, 06/07/1989, IAVH5918
64. Leticia, [4°11′36.11″S, 69°56′28.64″W], col. A. Villa-L., ND, IAVH5562; col. J. Garcés, 10/08/1973, IAVH1507; col. O. Pinto, 13/04/1986, IAVH6144
65. Amacayacu National Park, Estación Ecológica Omé, R. Purité,

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Part III
Ex Situ Research

Chapter 4
Behavior and Husbandry of a Captive Group of Woolly Monkeys: A Case Study

Brent C. White and Silvia Zirkelbach

Abstract With the addition of six woolly monkeys to its colony in the mid-1980s, the Louisville Zoo began a decade of successful breeding with 21 live births. We also initiated a systematic study of behavioral and environmental correlates of urinary cortisol excretion with the goal of understanding factors that contribute to hypertension in captive woolly monkeys. Urinary cortisol had a curvilinear relationship with social standing as measured by scream incidents. Cortisol was higher in females than males. Cortisol increased as females approached the normal term of their pregnancies. Three breeding females showed an association between cortisol and visitors, which may be confounded by ambient temperature. Otherwise, season, age, and housing condition (bachelor, breeding, mixed nonbreeding) did not affect cortisol excretion. Several varieties of social greetings were observed during calm interactions as well as after conflicts. Proximity among individuals reflected matrilineal grouping for mother-raised monkeys. Species-typical behaviors such as chest rubbing, predation, and social greetings were consistent with these behaviors as described in wild populations.

Keywords Woolly monkey husbandry · Cortisol in woolly monkeys · Captive woolly monkey behavior

4.1 Introduction

In the 1960s, the increasingly affluent societies of North America and Europe imported thousands of primates for sale as household pets. Woolly monkeys were among the most valuable exotic pets (Soini 1972; Thorington 1972), often referred to as the “Cadillac” of monkey companions.

Exotic pets often require more care and patience than common domestic animals. The high cost of maintenance in addition to injuries from aggressive pubescent males led many of these monkeys to be donated to zoos. The changing ethos

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B. C. White (✉)
Centre College, Danville KY 40422, USA
e-mail: brent.white@centre.edu

S. Zirkelbach
Louisville Zoo, Louisville KY 40213, USA

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Table 4.1 Live births at Louisville Zoo from 1985 to 2002

Date	Sire	Sire's origin	♀ births	♂ births	Hand-reared
1985–1987	WE	Wild born	2	0	0
1987–1992	HR	Captive born	3	10	4
1993–1996	PN	Wild born	3	0	1
	Unk	Captive born	0	1	1
1998–2002	CR	Captive born	1	1	1
Totals			9	12	7

among zoos encouraged conservation and preservation of their charges. With very limited success, zoos tried to breed these monkeys, which had been raised as surrogate children in diapers and highchairs. These former pets lacked experience with conspecifics, which appears to have affected their reproductive responsiveness—especially the females.

Also during the mid-twentieth century, several private collections of woolly monkeys were established outside of habitat countries. One of these was owned by Herbert Dornbrack and was eventually located at the Loch Lomond Wildlife Park in Scotland. In 1985, Dornbrack sold six of his animals to the Louisville and Los Angeles zoos to be housed at the former institution. The four adult females, a 2-year-old female and a 1-year-old male joined an adult male and his 3-year-old daughter in the Louisville exhibit. The adult male at Louisville had been wild-caught as an infant and then raised as a pet until he attacked his owner's wife. At this point, he was given to the Louisville Zoo, where he demonstrated he could breed with other woolly monkeys, in spite of his highchair experiences. This Louisville group became the most successful breeding group in North America.

Prior to 1985 when the Louisville Zoo woollies were predominantly ex-pets, many pregnancies resulted in miscarriages. In contrast, from 1985 to 2002, the Louisville Zoo managed a successful breeding colony, resulting in 21 live births and one miscarriage. Consequently, in 1988, the Zoo was awarded the prestigious Edward H. Bean Award for the propagation of woolly monkeys. Three females were responsible for most of these births. CN delivered six with a mean birth interval of 16 months, KZ had seven offspring at a mean interval of 22.5 months, and ZY had six at a mean interval of 18.6 months. The fecundity of these females exceeded the majority of breeding captive females (Mooney and Lee 1999). The sire, sex, and rearing conditions for the Louisville-born monkeys are summarized in Table 4.1. Although seven of these infants were hand-reared for various reasons, we successfully returned two infant males to their mother through careful management of the maternal–infant bonding (Logsdon 1992).

4.2 Methods

Fifteen months after the 1985 arrival of the six monkeys from Scotland, we commenced a behavioral study of the Louisville group, which included several types of systematic observations along with the collection of urine samples for cortisol assessment. During the first year of this study, observations were conducted several times each week (hours of observation = 1,197.2 across 135 days). In subsequent years, the systematic observations were limited to the summer months and continued through the summer of 1993.

An impetus for our study was the expanding evidence that woolly monkeys are particularly vulnerable to hypertension. Giddens et al. (1987) documented the histological evidence for hypertension in captive North American woolly monkeys. Muller et al. (1989) confirmed this result following an examination of woolly monkey kidneys in Europe. Elevated urinary cortisol is a correlate of essential hypertension in humans, which has been shown to decline as psychological manipulations reduce stress (McGrady et al. 1981). Given the apparent similarity in hypertension between humans and woolly monkeys, we set out to find behavioral, environmental, and demographic correlates of urinary cortisol excretion in the monkeys of the Louisville colony.

We were also interested in describing the captive behavior of this species, using systematic observational techniques. Leonard Williams had written several books (e.g., Williams 1968) describing the behavior of captive woolly monkeys. However, his disdain for the scientific study of behavior led him to avoid systematic, objective procedures. We employed these techniques to provide a basis for hypothesis testing and for comparing the behavior of captive animals to their wild counterparts.

4.2.1 Correlates of Cortisol Excretion

Although cortisol can be found in virtually all body fluids and in feces, we chose to measure urinary cortisol because of the availability of a reliable assay and the noninvasive collection procedures. We have used the Coat-A-Count radioimmunoassay for cortisol that is marketed by Siemens Medical Solutions Diagnostics, Los Angeles, CA, USA. Our collection, storage, and quality control procedures were described in White et al. (2010). The cortisol results reported in this chapter are based on the use of specific gravity to correct the urine samples for variation in urine volume and concentration of solutes. See White et al. (2010) for a discussion of this issue. Specific gravity was measured using a refractometer and converted to a one- or two-digit whole number by subtracting 1.0 and multiplying by 1,000. When correcting cortisol concentration for urinary dilution, we used the normal or mean value of the specific gravity (6.7) divided by the sample specific gravity and multiplied the result by the sample cortisol concentration (Levine and Fahy 1945).

During five veterinary examinations, we were able to collect samples of urine, saliva, and serum that were obtained over a span of a few minutes. Although the number of samples was small, this procedure has allowed us to directly compare these three body fluids. Serum cortisol concentration correlated most strongly with the concentration in the urine ($r=0.96$, $p=0.01$) and next with the specific-gravity-corrected urine concentration ($r=0.87$, $p=0.05$). The serum values were not significantly correlated either with the salivary concentration or with the creatinine-corrected urine concentration.

4.3 Results, Discussion, and Conclusions

4.3.1 *Cortisol and Season*

Maintaining tropical animals at temperate latitudes raises the possibility of seasonal influences on the animals that would not be seen in their native habitat. We examined the effect of season on cortisol excretions with a robust number of animals (15–19 represented in each season) and found no statistically significant differences among the seasons. This was also the case when we looked at females and males in separate analyses. We have no evidence from our studies that the fluctuations in photoperiod and weather associated with a latitude of approximately 38°N have any effect on cortisol excretion. This is the case in spite of several potential stressors that might be expected to correspond with seasonal changes—crowding due to confinement during winter, colder environmental temperatures during winter months, and the increase in visitors during summer months. Two females showed moderately positive correlations between ambient temperature and cortisol excretion (CN: $r = 0.68$, $\mathrm{df} = 14$, $p < 0.01$; ZY: $r = 0.66$, $\mathrm{df} = 13$, $p < 0.01$). Of course, these correlations are confounded by the number of visitors as seen below.

4.3.2 *Cortisol and Visitors*

When animals are maintained in a facility that is open to the public, there is the potential for visitors to affect the well-being of the animals. A common assessment of well-being has been cortisol excretion (Carlstead 1996; Mason and Veasey 2010). We had eight animals for which there were six or more samples that had specific gravity and visitor data from the day of the sample and the previous day. Table 4.2 summarizes these results.

For three females, specific-gravity-corrected cortisol was positively correlated with the previous day's visitors, suggesting that some of the monkeys were affected by the public. Two of these females were mentioned above as showing a positive correlation between daily temperature and cortisol. A fourth female, SR, showed a negative correlation. SR was never on exhibit, so her reaction may be mediated through activity of the keepers. She was housed in an area where she had frequent interactions with the keepers. Perhaps, on days with large numbers of visitors, the keepers had less time for her.

4.3.3 *Cortisol Excretion under Varied Grouping*

The initial study group was a breeding group with an adult male, three adult females, and two juveniles. During later study periods, some animals were housed in mixed nonbreeding groups and in all-male bachelor groups. Surprisingly,

Table 4.2 Correlation between urinary cortisol and number of visitors

ID	Sex	Age	N	Correlation coefficients		Mean cortisol	
				Visitors on day prior to sample (r)	Visitors on day of sample (r)	Concentration (µg/dl)	SG corrected (µg/dl)
CN	F	8	16	0.65**	0.62**	31	57
KZ	F	7	31	0.47**	0.04	25	45
ZY	F	5	15	0.59*	0.56*	20	37
FX	M	3	7	0.50	−0.28	27	24
PB	F	1	6	0.30	0.34	24	28
HR	M	8	7	0.45	0.45	14	21
SR	F	5	26	−0.40*	0.07	36	36
TM	M	6	55	−0.02	0.04	20	23

*$p \leq 0.05$, **$p \leq 0.01$

cortisol excretion was not affected by these arrangements. The mean specific-gravity-corrected cortisol was not significantly different across the three conditions (breeding 35.0 µg/dl ± 4.4 standard error of mean (sem), mixed 30.4 ± 4.8, and bachelor 31.4 ± 4.4).

4.3.4 Cortisol Excretion by Sex and Age

Figure 4.1 shows the mean cortisol in 2-year age blocks for males and females. Overall, females (mean ± sem = 38.8 ± 4.4, $n=6$) exhibited significantly higher cortisol excretion than males (mean = 26.8 ± 2.3, $n=11$; $T=2.68$, df = 15, $p=0.02$). However, there were no consistent age-related changes in cortisol excretion. Of the 17 monkeys, 11 were represented in more than one 2-year age block. In order to assess longitudinal changes in cortisol excretion, we determined whether the individual showed an increase in cortisol from its youngest to its oldest age block, and then used a proportion test to evaluate whether a significant proportion of the monkeys increased. Of 11 monkeys, 6 increased their cortisol excretion, which was no better than what we would expect from chance ($Z=0.32$, $p=0.75$).

4.3.5 Cortisol Excretion during Pregnancy

Three pregnancies occurred at times when we were able to obtain specific-gravity-corrected cortisol. CN had two of these pregnancies and KZ had one. In Fig. 4.2, we have combined the pregnancies to illustrate the increasing cortisol excretion as the mothers approached the time of birth, which is represented at the left end of the horizontal axis. All of these females exhibited frequent drinking and urinating. Ziegler et al. (1995) reported a similar increase for cotton-top tamarins as parturition approached.

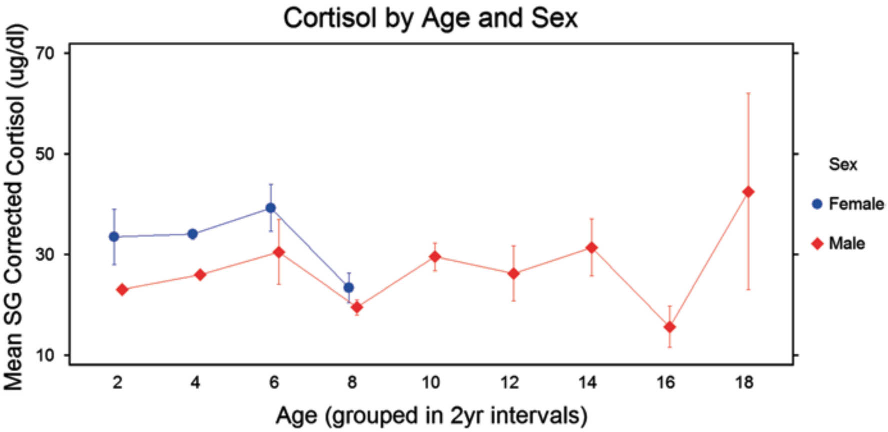

Fig. 4.1 Mean specific-gravity-corrected urinary cortisol (±sem). Ages are grouped in 2-year intervals. Males and females are illustrated separately

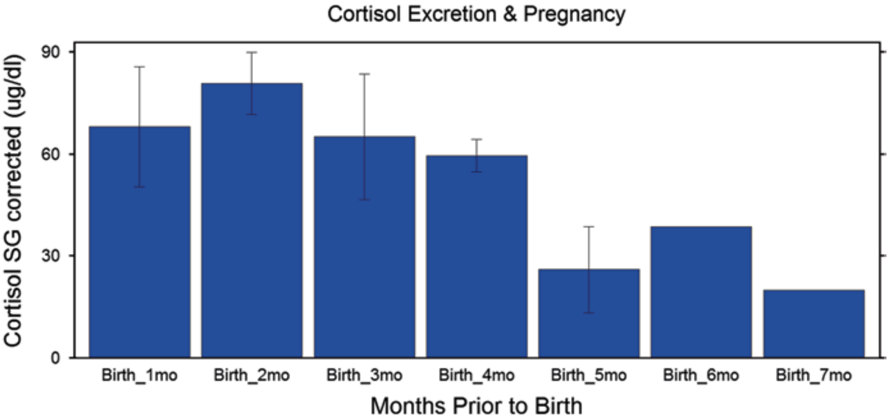

Fig. 4.2 Mean specific-gravity-corrected urinary cortisol (±sem) at monthly stages of pregnancy, beginning at the left with the month immediately prior to birth

4.3.6 Cortisol and Social Rank

Figure 4.3 shows the curvilinear relationship between cortisol excretion and the scream index of social standing (SISS) as measured by the percentage of scream incidents that a monkey was screamed at. The two adult males at the high end of the social standing index almost never screamed at another animal, giving them the highest ratings. These two males were not in the group at the same time. The reproducing females, a subadult female, and a juvenile male were in the middle range of social standing and had the highest cortisol excretion. The high mortality among

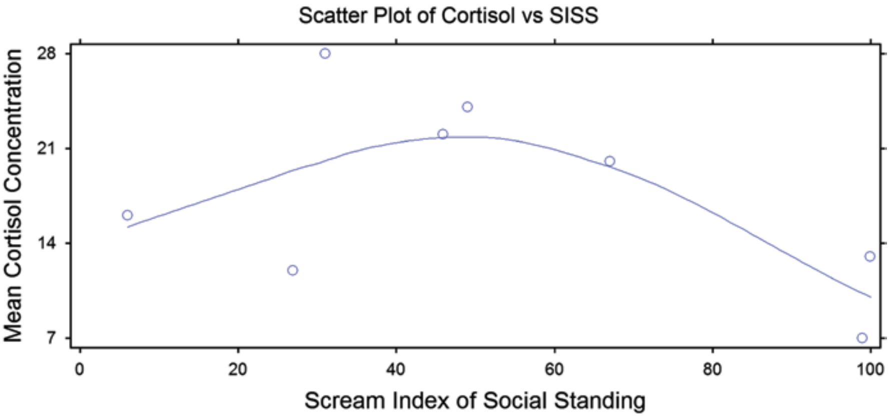

Fig. 4.3 Mean urinary cortisol concentration and social standing during the first year of the study. Scream incidents were used to determine social standing, reflecting the percentage of scream bouts in which the individual was screamed at

captive reproducing females (Mooney and Lee 1999; Ange-van Heugten 2008) may be related to high cortisol, which may reflect social and environmental stressors. In addition, the three females which collectively accounted for 86 % of the births were in this group with high urinary cortisol. These three females also showed significant correlations between visitors and cortisol excretion. For two of them, temperature was correlated with cortisol as stated above.

4.3.7 Social Behavior

Our study of the social behavior of the Louisville woolly monkey colony has included qualitative descriptions of social interactions and quantitative analyses based on systematic observations. We have not studied the varied vocal repertoire of these animals due to limitations imposed by the structure of the exhibit. A glass barrier between the animals and the public made it difficult to hear the quiet vocalizations and impaired localization of the louder calls.

Method for Behavioral Observations Focal instantaneous recording provided information on the social proximity of the focal animal every 60 s of a 30-min observation period. Observations were scheduled for even distribution across seven 2-h time blocks. A random order of observations provided a near-equal number of sessions for each animal at each time period when distributed over several days. Proximity was scored in four categories: contact, within reach, nearest, or alone. This latter category meant that the focal animal was alone on an island or in one of the indoor rooms. The identity of the other animal was also recorded.

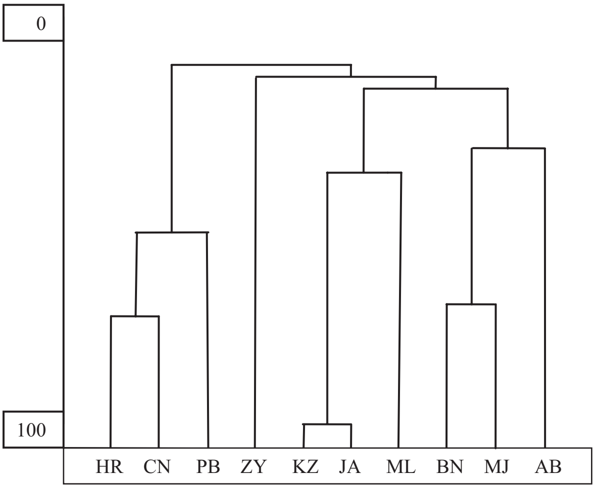

Fig. 4.4 Dendrogram showing associations among group members during the summer of 1989. Higher numbers on the *y*-axis indicate close associations between individuals. Horizontal lines indicate strength of the association as per the *y*-axis scale

Social Proximity Nearest-neighbor results were converted to an association index (AI) where the number of scans that two animals were nearest was divided by the total scans that each individual of the pair was nearest to other animals. The result was multiplied by 1,000. Using all possible pairs of animals, a single-link cluster analysis (SLCA) was conducted for each of five periods during the first year of our study and for each subsequent summer of observations. This is a hierarchical procedure (Morgan et al. 1974) where the animals with the highest AI are associated near the bottom of a dendrogram as seen in Fig. 4.4. The next highest AI is connected with a horizontal bar that is elevated proportionately on the *y*-axis. Vertical lines show the individuals involved at each level. This continues until all animals are included. The dendrogram illustrates the closest relationships and the degree of association among group members.

Figure 4.4 shows the dendrogram for the summer of 1989. We selected this year to illustrate the typical associations when there was an adult male in the group. As expected, young animals were associated with their mothers. Two distinct matrilines can be seen in Fig. 4.4. KZ, an adult female, shows the strongest association in the group with her 5-month-old son, JA. KZ's next strongest association is with her 2-year-old daughter ML, completing KZ's matriline in 1989. CN, also an adult female, was mating with the adult male HR during this period, showing the next strongest association after KZ and JA. CN's next closest association was with her 2.5-year-old daughter, PB. Earlier in 1989, CN had given birth to a son, BN, but the infant was removed from the group for a week of medical treatment. Upon return to the group, CN did not accept BN, who was then hand-raised, spending part of each day in the group. ZY was also a reproducing female, having given birth to a son, MJ, and a daughter, AB. ZY did not nurse either of these infants, so they were also hand-raised, but returned to the group. ZY shows no close associations. The three hand-raised monkeys (BN, NJ, AB) show their closest associations with each other.

4.3.8 Conclusions from SLCA

1. Matrilineal associations dominate proximity relationships.
2. Within matrilines, the strength of associations decreases with the age of the offspring.
3. Among juveniles, males are more likely to associate outside of matriline than females.
4. Mothers do not associate, perhaps recognize, hand-raised offspring.
5. In the absence of an adult male, matrilines are less distinct.

As with our results, in wild groups, close proximity is most commonly found between mother and offspring (Stevenson 1998; Nishimura 1997). Nishimura describes these maternal associations as weakening with age, but persisting for up to 3 years. Our hand-reared monkeys are analogous to orphaned monkeys that have been returned to wild groups. Unfortunately, we do not have information on the associations that are formed with these reintegrated orphaned monkeys.

Social Greetings We observed social greetings between two or more individuals that involved a variety of body postures. A head-to-head greeting occurred when two animals going in opposite directions passed each other on a ramp or log. Their heads were briefly placed touching ear to ear or cheek to cheek for a few seconds, often <10 s. The head-to-chest greeting had two variants, including one similar to the head-to-head but with the head placed near the armpit of the other animal. The other variant involved one animal seated and the other approached and placed his/her head on the chest of the seated animal. In a third type of greeting, the greeter laid in front of the seated or standing animal for a few seconds. The recipient ignored or briefly lay over the greeter. A fourth type of greeting involved the greeter facing the recipient with a hand or arm over the greeter's mouth or face. This greeting was sometimes answered with the same gesture or with no apparent reply other than a change in the ongoing behavior such as a cessation of screaming. The final form of greeting often involved more than two animals and has been called a snuffle or huddle. In this case, several animals huddled on a flat substrate for up to a minute or two. The huddle often ended with playful wrestling among some of the participants.

During the first year of our study (September 1986 through August 1987), we observed 293 greetings. Of these greetings, 45 occurred during or shortly after an intense social encounter involving a fight, a scream incident, or mating. The use of the greeting during and after fights and scream encounters suggests that the greetings offer a means of reconciliation among animals in conflict. On several occasions, a 2-year-old male was grappling with an unrelated adult female. The play got too rough for him and he screamed, which brought his mother to the area and this resulted in the adult females screaming at each other. The young male placed himself between the females and greeted each, usually with his hand over his mouth. This gesture appeared to resolve the conflict.

Although some greetings were associated with conflicts and mating, many others occurred when no immediate social event was identified. Most greetings involved and were initiated by adult females. Greetings occurred among matrilineal members and across matrilines.

In 1996, the colony suffered a dramatic decline when four females and three males died from an unidentified virus. The resulting imbalance in sexes led to the establishment of a male bachelor group in the summer of 1998. Initially, there was considerable conflict, which was documented by the high number of scream incidents and bite wounds. The group was established with six animals. For several years, JY remained the dominant animal. He and three younger males, with whom he had grown up, often greeted each other during and after bouts of screaming and fighting. The most common forms of greeting were the hand over mouth and the head to chest or armpit. MJ, a member of the group for 12 years, protected three younger monkeys as they were introduced by jumping into conflicts and screaming at the chaser in a manner suggestive of de Waal's (1990) description of peacemaking.

In the bachelor and the breeding groups, greetings appear to reinforce bonds between familiar animals. This is similar to the apparent function of embraces among captive spider monkeys (Schaffner and Aureli 2005).

Comparison of Captive and Wild Behavior The captive environment is necessarily artificial and limited when compared to the spatial opportunities and the physical and biological complexity of the natural habitat. However, by examining the similarities and differences in behavior, we can get a sense of the stability of the behavior across environments and/or the extent to which the captive environment approximates the natural habitat. Social behavior can be observed more easily in confinement, which may provide greater detail. The variety of greetings that we have observed supports this interpretation. Ramirez (1988) has reviewed captive and habitat studies, providing an impressive list of behaviors. The social greetings in her list come largely from captive studies (Williams 1968, 1974). Two of these, sobbing and snuffling, are similar to the hand-to-mouth (snuffling) and the huddle greetings that we have observed. Oral neck nuzzling was observed in wild woolly monkeys by Kavanagh and Dresdale (1975). This approximates our head-to-head greeting. The greater variety that we have seen may be due to the compression of social interactions produced by the limited space of a relatively small captive enclosure.

All-male bachelor groups have been observed in the natural habitat of woolly monkeys (Di Fiore and Fleischer 2005); however, they are rarely reported, so we know virtually nothing of the social interactions within these groups. From the study of large multi-male, multi-female groups, adult males avoid close proximity to other males (Di Fiore and Fleischer 2005; Stevenson, 1998) and are more likely to interact directly with females (Nishimura 1994). Thus, when a bachelor group was established at the Louisville Zoo, there was considerable tension as evidenced by the relatively high incidence of scream encounters and chest rubbing (White et al. 2003). The subsequent decline in these behaviors suggests an accommodation similar to the spacing among males in the wild.

Captive woolly monkeys are well known for chest rubbing on a variety of substrates, which was interpreted by Williams (1968) to be territorial marking. Our observations (White et al. 2000) showed that chest rubbing was largely an adult male behavior that was related to reproductive activity. This was confirmed by studies conducted in two locations in Colombia (Di Fiore et al. 2006).

Woolly monkeys are considered frugivores (Stevenson 1992; Defler and Defler 1996; Dew 2005), but they are also well known to prey on invertebrates and occasionally vertebrates. We documented bird predation by the monkeys of the Louisville Zoo (Stearns et al. 1988). Other captive groups of woolly monkeys have also been reported to prey on birds (Clarke and Mitchell 1982; Williams 1968). In our study of the Louisville group, a captured bird was frequently pursued, stolen, and/or torn apart as members of the group attempted to get part of the prey. Pursuit of a monkey with a captured bird was correlated with the social status of the pursuing monkey. One of the most interesting findings from this study was the high incidence of fiber consumption along with the flesh of the bird. Fiber sources included wood from trees in the exhibit, wood molding inside the stall areas, bark, straw, and frayed rope. The pattern of consumption alternated between flesh with long bouts of chewing and a source of fiber. Subsequent to our report, Stevenson (1992) described an adult female in Colombia alternating between feeding on a lizard and consuming mature leaves. This appears to be similar to the "wadging" behavior of chimpanzees described by Teleki (1973) and also reported by Nishida et al. (1979). However, the leaves used in wadging are rarely consumed, whereas the fiber eaten along with the flesh of the birds by the Louisville monkeys was swallowed. In describing her first observation of meat eating by chimpanzees, Goodall (1971) noted that an adult male alternated between consumption of the flesh of a piglet and nearby leaves. This latter account suggests that chimpanzees were using leaves in the same manner as the Colombian and Louisville woolly monkeys. The addition of fiber and course plant material may aid the digestive process. Further study is needed to clarify the potential digestive functions of the fiber and also to identify the sensory trigger for switching between flesh and fiber.

In conclusion, the comparison of captive and wild behavior provides a measure of the quality of the captive environment (Veasey et al. 1996). Our studies of the Louisville group of woolly monkeys document that their expression of social behaviors, environmental marking, reproductive behavior, and predation is similar to the behavior of this species in its natural habitat. The approximation of natural conditions in the Louisville exhibit is close enough to permit many natural behaviors. It remains to be determined whether the pattern of hypertension and glucocorticoid excretion in these captive monkeys is also reflected in wild populations.

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Chapter 5
Clinical Experience and Diseases of the Woolly Monkey (*Lagothrix lagothricha*) at the Louisville Zoo

Roy Burns

Abstract This chapter summarizes the clinical experience and observations made in providing health care to woolly monkeys at the Louisville Zoo, Louisville, KY, USA, during the period 1990–2012. Several significant diseases have been observed in this zoo population of woolly monkey, including hypertension and related disease, woolly monkey hepatitis B virus, ascending paralysis, toxoplasmosis, dental disease, and endoparasitism. Louisville Zoo is the only zoo to house a large number of breeding woolly monkeys in the USA.

Keywords Woolly monkey health care · Health captive woolly monkeys · Disease captive woolly monkeys

5.1 Preventative Health of *Lagothrix* at the Louisville Zoo

A rather aggressive approach of preventative health care has been taken to better understand medical issues in *Lagothrix* at the Louisville Zoo. Preventative health exams are performed under general anesthesia every 1–3 years and include: (1) echocardiography; (2) complete blood count, serum chemistries, and serology; (3) blood pressure (direct and indirect); (4) electrocardiogram; (5) radiographs and evaluation of vertebral heart sum; (6)tuberculin testing; (7) fecal culture; and (8) vaccinations. In addition, some procedures are performed via trained cooperation from the monkeys on a more regular basis: observation for anomalies, urine collection with resulting urinalysis and cortisol measurements, and indirect blood pressure measurement.

R. Burns (✉)
Louisville Zoological Garden, 1100 Trevilian Way, Louisville KY 40213, USA
e-mail: Roy.Burns@louisvilleky.gov

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5.2 Hypertension and Hypertension-Related Disease

Hypertension in the woolly monkey has been described in the literature since the 1960s (Andrus and Portman 1966; Giddens et al. 1987; Muller et al. 1989; Miller et al. 1995; Wagner et al. 1984). The disease appears to be similar to essential hypertension in humans, meaning the cause of the hypertension is not known.

A survey of woolly monkey health in US zoos published in 1987 (Giddens et al. 1987) showed the following:

1. All hypertensive monkeys were >4 years of age.
2. Of 38 monkeys, 17 died of hypertension-associated disease (congestive heart failure, renal failure, and/or cardiovascular accident).
3. Arteriolar nephrosclerosis was observed at necropsy in 26 of 38 woolly monkeys.
4. Direct arterial systolic blood pressures measured under ketamine restraint were 194+/−20 mmHg. Guidelines on evaluating blood pressures used by the American Heart Association at that time were used to classify pressures as hypertensive.

A publication from the Basel Zoological Garden in 1989 identified arteriosclerosis in the kidneys of 15 woolly monkeys (Muller et al. 1989). Arteriosclerosis is one of the end-organ pathologies associated with hypertension in humans. Authors speculated there may be multiple causative factors of hypertension in the species including obesity, restricted physical activity, stress, diet, and genetic/species vulnerability.

Published measurements of blood pressure in free-ranging woolly monkeys are nonexistent. However, pathology typically caused by hypertension has been observed in free-ranging or newly captured woolly monkeys. Necropsy findings in eight recently captured woolly monkeys describe arteriosclerosis in one monkey and vena caval thrombosis in two monkeys (Henderson et al. 1970). A comparative study of pathology in primates which included 15 *Lagothrix* killed in their native habitat identified more aortic atherosclerosis in *Lagothrix* compared to others (*Cebus, Saimiri, Callicebus, Alouatta*) (Andrus and Portman 1966). Therefore, hypertension in free-ranging woolly monkeys is likely and has been established in free-ranging individuals of other primate species (rhesus monkeys, *Macaca mulatta*) (Modi and Chakravarti 1975).

Clinical diseases observed associated with hypertension were as follows: myocardial fibrosis, myocardial hypertrophy, myocardial dilation, congestive heart failure, pericardial effusion, arteriosclerosis, arteriolar nephrosclerosis, thrombosis/thromboembolism, and aneurysm.

Diagnostic testing for hypertension and hypertension-associated disease in woolly monkeys has included the following tests: indirect blood pressure measurement via training, urinalysis (specific gravity, protein-to-creatinine ratio), direct and indirect blood pressure measurement under general anesthesia (ketamine), radiography (vertebral heart sum), echocardiography, and cortisol measurements.

Louisville Zoo has attempted to better understand hypertension in the species with little result. In the 1990s, Louisville Zoo performed a three-part Institute of

Museum Services (IMS)-funded study to better understand woolly monkey health issues related to hypertension (Burns 1997). The study consisted of a historical medical survey, diagnostic evaluation of ten woolly monkeys, and a pilot project with the Pittsburgh Zoo, Pittsburgh, PA, USA, to determine if radio telemetry would be a viable tool to measure blood pressure in an unrestrained woolly monkey.

The survey included pathology reports from postmortem examination of 74 woolly monkeys housed at several zoos. Of the 74 woolly monkeys, 52.7 % had cardiovascular disease, 52.7 % had renal disease, 37.8 % had liver disease, 12.2 % had lung disease, and 12.2 % had colitis found at necropsy. The most common antemortem-diagnosed cardiovascular diseases were cardiomegaly and myocardial hypertrophy. Using Pearson correlation coefficients, a significant correlation between age and the presence of hypertension and between age and the presence of cardiovascular disease was observed (Burns 1997).

Guidelines on evaluating blood pressures used by the American Heart Association at that time were used to classify whether pressures were hypertensive. Systolic pressure above 139 mmHg and diastolic pressures above 89 were considered hypertensive. This is similar to a classification of rhesus monkey blood pressures in which individuals were considered hypertensive if systolic blood pressure was above 140 mmHg and diastolic blood pressure was above 90 mmHg (Modi and Chakravarti 1975).

Diagnostic evaluation of ten woolly monkeys housed at the Louisville Zoo showed all were hypertensive with mean direct blood pressures of 179.5 mmHg systolic (range 141–242 mmHg) and 119.7 mmHg diastolic (range 90–195 mmHg). Other parameters measured in which woolly monkey results were higher than published human normal ranges included serum cortisol, epinephrine, and dopamine. Parameters measured in woolly monkeys that were normal compared to human ranges included plasma rennin activity, aldosterone, and insulin.

Two woolly monkeys had their blood pressure monitored by radio telemetry and an implantable device measuring blood pressure in the femoral artery. Both monkeys recovered to normalcy after implant removal. The implant in the first monkey failed in 2 days. The implant in the second monkey successfully recorded blood pressure for 40 days after which the catheter pip became clotted, likely from the catheter not being advanced far enough into the artery. Blood pressure measured by telemetry showed a significant circadian rhythm (high daytime, low nighttime).

Diet evaluation and diagnostic testing of six woolly monkeys with known hypertension problems determined that diabetes mellitus and nutrition were not associated with hypertension in the species (Ange-vanHugten et al. 2007).

The role of cortisol in woolly monkey hypertension is suspect. Woolly monkeys appear to have high circulating levels of cortisol compared to other nonhuman primates (White et al. 2010). The role of cortisol in hypertension has been partially investigated, especially in humans (for example, Whitworth et al. 1995; Van Itallie 2002; Anagnostis et al. 2005). Metyrapone inhibits production of cortisol, corticosterone, and aldosterone by blocking 11B-hydroxylase in the adrenal cortex and therefore this inhibitor was studied as a potential way to decrease cortisol.

In 2010, Louisville Zoo administered metyrapone at therapeutic doses (25 mg/kg orally twice a day) to a single woolly monkey in hopes of reducing circulating salivary cortisol and measuring blood pressure in a woolly monkey with low cortisol. However, administration did not result in a reduction of salivary cortisol or blood pressure (measured via training) of the captive animals at Louisville.

Despite high doses of every major class of antihypertensive drug used in humans, no treatment has been found that significantly reduces blood pressure in hypertensive woolly monkeys at the Louisville Zoo. Medications used in an effort to reduce blood pressure in woolly monkeys at the Louisville Zoo have included: (1) diuretics (furosemide); (2) hydrochlorothiazide (spironolactone); (3) ACE inhibitors (enalapril, captopril, lisonopril); (3) calcium channel blockers (amlodipine, diltiazem); (4) beta antagonist (atenolol, propranolol, metoprolol); (5) alpha 2 adrenergic agonists (clonidine); (6) mixed alpha/beta adrenergic antagonist (lobetalol, carvedilol); (7) direct vasodilators (minoxidil, nitroglycerine); (8) sympatholytic drugs (methyldopa); (9) cardiac glycosides (digoxin); (10) herbals (graviola, *Annona muricata*; rainforest herbal blend hypertension formula); and (11) aspirin, vitamin E, and flaxseed oil.

5.3 Woolly Monkey Hepatitis B virus

In 1997, a 10-year-old female woolly monkey housed at Louisville Zoo died from liver disease. Antemortem and postmortem diagnostics resulted in the discovery and description of a new hepatitis B virus, woolly monkey hepatitis B virus (WMHBV). The genome organization of the virus was described by Dr. Robert Lanford, SW Foundation for Biomedical Research (Lanford et al. 1998). He observed that the nucleotide sequences of core and surface genes indicated that WMHBV is a distinct hepatitis B virus (HBV) and may be a progenitor to human HBV.

At that time, 18 woolly monkeys remained at the Louisville Zoo. Of the 18, serological tests and polymerase chain reaction (PCR) using primers from a highly conserved domain overlapping the core gene showed:

1. Chronic infection (six monkeys)
2. Cleared previous infection (three monkeys)
3. No infection (four monkeys; two monkeys living at the time of index case and two monkeys born since the death of the index case)
4. Unknown infection status (one monkey)

Since the identification of WMHBV, ten monkeys have died and have shown no viral hepatitis pathology. These monkeys were:

1. Chronically infected (five monkeys)
2. Cleared of previous infection (three monkeys)
3. Of unknown infection status (one monkey)
4. Not infected (one monkey)

Since the identification of WMHBV, an employee health testing and vaccination for hepatitis B has been implemented. Serological tests showed no employee was exposed to the virus; thus, no employee could have been the hepatitis origin.

A serosurvey for WMHBV was performed on 80 serum samples representing 43 woolly monkeys from 11 locations. The serosurvey identified 23 monkeys (53 %) testing positive for infection via PCR, HBsAb, HBcAg, and/or HBcAb. All had been held at either Louisville Zoo or another location housing woolly monkeys that were once held at the Louisville Zoo. Interestingly, the earliest positive serum sample was collected on 3 November 1987 and corresponded with the importation of a family group (five monkeys) from Dumbartonshire, Scotland, in July 1985. Correspondence and serologic testing led to a European zoo believing WMHBV entered their collection via the same source. No details are available to me regarding follow-up on those animals.

5.4 Ascending Paralysis

In 1996, the Louisville Zoo experienced the acute death (sudden death) of four woolly monkeys (two in the morning and two in the evening) with rapid progressive weakness as the only antemortem clinical sign. Three additional monkeys died over the next 6 days. These monkeys all showed weakness, lethargy, ascending paresis/paralysis, and fever prior to death. Of the remaining monkeys, four became ill and recovered, and one showed no symptoms. Pathology findings were unrewarding with respect to a causative factor.

A viral culture showed a cytopathic effect similar to an enterovirus but the virus did not survive transport to another laboratory for further identification. The pattern of the outbreak suggests a point source, and there was a history of a sewer backup in the woolly monkey service hall 7 days prior to the outbreak in which material appearing to be pieces of a disposable diaper was found. Poliovirus is an enterovirus with an incubation period of 7–10 days, and oral live vaccines were commonly administered to human infants at that time (Alexander et al. 2004). Human infants administered oral live polio vaccine shed the virus in saliva and feces for several weeks. Although it is highly speculative, attending veterinarians suspect the sewer backup may have contained feces from an infant recently treated with an oral polio vaccine.

5.5 Toxoplasmosis

Toxoplasmosis is caused by infection with the protozoan (coccidian) parasite *Toxoplasma gondii*. More than 200 species of birds and mammals can act as intermediate hosts for this protozoan. Domestic and exotic felids are the only known definite hosts capable of shedding the parasite in the feces (shed oocysts become infectious after 1–5 days of exposure to oxygen). For intermediate hosts, the severity of infection is typically higher in some species and new-world primates, including the woolly monkey, are unfortunately included (Bouer et al. 1999; Hessler et al. 1971). Louisville Zoo has diagnosed toxoplasmosis as the cause of death in two woolly monkeys (2000 and 2002). Both had multiple-organ dissemination of the organism. One monkey showed a peracute illness and death and the other monkey showed a weeklong illness and death. Exposure is most likely from either consuming infected prey (birds, mice) or being exposed to infected feral cat feces.

5.6 Other Management Concerns/Diseases

In older woolly monkeys, the occlusal surfaces of teeth become so worn that dental pulp and nerves become exposed and the teeth become sensitive. Several monkeys have been treated for this by a root canal procedure typical of human dentistry.

Enteric parasites diagnosed in woolly monkeys at the Louisville Zoo include: (1) protozoans (*Trichomonas*, *Giardia*) and (2) nematodes (strongyles) and pinworms (*Enterobius* sp.). These parasites are treated by routine and as needed anthelminthics.

Itching and irritation of the vulva has been observed in some female woolly monkeys post partum. Symptoms have been relieved by administration of a urinary anesthetic (phenazopyridine). In addition, seasonal itching has been observed in a woolly monkey. Symptoms were relieved by administration of an antihistamine.

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Chapter 6
Recent Advances in Woolly Monkey Nutrition

Kimberly D. Ange-van Heugten

Abstract Woolly monkeys (*Lagothrix* ssp.) are threatened in the wild and are extremely difficult to successfully manage within captivity. The majority of health problems in woolly monkeys (WM) may be of dietary origin. We demonstrated that captive WM decreased by 11 % during a 16-year period. In addition, the number of captive facilities reportedly holding WM diminished while the birth-to-death ratio was inverted at 0.65 compared to 1.26 for the similar spider monkey (SM; *Ateles* spp.) species. When examined, the historical serum chemistry data from 30 WM housed at two captive facilities did not differ when compared to published results for howler monkeys (*Aloutta* sp.) and SM. However, serum glucose was elevated compared to humans and SM. Further research demonstrated that fasting levels of circulating lipids, fructosamine, glucose, glycated hemoglobin, insulin, and urinary glucose were normal in six WM with known hypertension compared to published data from similar monkey species and humans. Potential stressors can contribute to decreased health status within primates. Our investigation of fecal and salivary cortisol in WM and SM showed that captive institutions with the highest dietary total carbohydrates, total sugars, glucose, and fruit content had the highest cortisol concentrations. Further, our supplementation of WM and SM diets with inulin-type fructans numerically lowered fecal cortisol after 4 weeks. It is possible that the success of captive WM could improve if stressors and potential negative consequences of improper nutrition are reduced.

Keywords Woolly monkey captive management · Cortisol · Diabetes · Diet · Health · Hypertension · Lipids · Nutrition · Serum concentrations · Stress

6.1 Introduction

The first zoo opened in ancient Egypt and zoos have since multiplied across the world to entertain and educate the public (Hanson 2002). The first zoos were designed for display of unique animals, and conservation was not a priority because most animals were easily replaced. As free-ranging animal populations became

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K. D. Ange-van Heugten (✉)
North Carolina State University, Raleigh, NC, USA
e-mail: kimberly_ange@ncsu.edu

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scarce, conservation slowly became a concern, and today conservation programs are integral aspects of zoological management. As part of this management, proper nutrition of captive animals became a priority. However, it is difficult to determine nutritional requirements for many species. This is a matter of concern because species that are endangered in the wild are likely to become extinct if our society cannot manage to properly feed and breed them in captivity.

Research with captive exotic animals is complicated because many species are scarce both in captivity and in the wild, and all situations that may increase their stress or be perceived as threats are limited by holding institutions. Moreover, many of these holding institutions do not allow diagnostic samples to be taken. Investigators are rarely allowed to change the animal's environment or diets as experimental treatments. Many traditional animal research methods call for animals to be isolated or separated into age- or gender-specific groups and this can be very stressful for wild animals. If collection of samples is allowed, transporting them among locations increases the risk of spreading zoonotic disease. This means specific permits are needed before endangered animals or their biological samples can be transported. Consequently, it is challenging to determine the nutritional requirements and diet-related health concerns affecting many species kept in zoological institutions.

The woolly monkey (*Lagothrix lagothricha*) is a species that is difficult to manage and feed in captivity. They are endangered in the wild to varying degrees across their subspecies and approximately 85 woolly monkeys are reported to live in captivity worldwide (Ange-van Heugten et al. 2010; CITES 2007). While these numbers do not account for many animals in South American rehabilitation centers, the captive numbers remain scarce compared to most new-world primate species. For example, 16,000 woolly monkeys were imported into the USA in the early 1960s and less than 10 remained in 2000 (Franceshini et al. 1997; Ange-van Heugten et al. 2010). Attaining a long (normal) life span (more than 15 years) for these monkeys in most captive locations throughout the world has had very limited success. The majority of their health complications are often thought to be captive nutrition or diet related. This conclusion being deduced, in part, due to their problems being similar to those of diabetes mellitus and hypertension in other primates. In particular, it is known that elevated levels of lipids, sodium, and sugars in human diets can increase the prevalence of type II diabetes and/or hypertension (Lagua and Claudio 2004). These two diseases also are closely related to other conditions reported to negatively affect woolly monkeys, including congestive heart failure, renal failure, reproduction problems, and immunosuppression (Ange-van Heugten et al. 2008b; Giddens et al. 1987; Miller et al. 1995). As with humans, these woolly monkey health conditions are often more pronounced during pregnancy and may result in very large, difficult-to-deliver, infants (Lloyd et al. 1995). These health problems have contributed to lowering the captive life span and seriously decreasing the captive population of woolly monkeys. Therefore, it is vital to better understand the nutritional needs and associated disorders within this species in order to determine whether the captive health problems can be prevented by feeding a nutritionally balanced and close to natural diet. It is critical to first understand the nutritional habits of free-ranging woolly monkeys. Compared to other primates, they spend a large amount of time eating and moving in pursuit of food (approximately 60–75 %; Dew 2005; Di Fiore and Rodman 2001; Di Fiore 2004). They are primarily frugivores, consuming fruits that are characterized by tough outer shells. Compared to their close relative, the spider monkey (*Ateles* sp.; Di Fiore and Campbell 2007; Ford and Davis 1992), they tend to eat fruits that are lower in fat and higher in both total sugars and water (Dew 2005). Woolly monkeys prefer harder fruits, consume more vegetative matter, forage in larger groups, consume from more plant species, and never forage from the ground as compared to spider monkeys (Dew 2005). It is likely that captive woolly monkeys are fed diets that do not provide enough non-starch polysaccharides or crude fibers, the reason being that fruits and vegetables cultivated for human consumption typically contain more water and sugar and less fiber and protein than those for their wild ancestors (Milton 1999). In addition, woolly monkeys are often fed diets similar to their close relative, the spider monkey (and other captive monkey species), which may be inappropriate. Approximately 1,000 spider monkeys are reportedly housed in captivity worldwide compared to the 85 woolly monkeys reported (Ange-van Heugten et al. 2010). Both species are considered threatened although only woolly monkeys are considered extremely difficult to maintain in captivity.

Considerable diet variation within the wild population of woolly monkeys exists even among the subspecies and across seasons (Defler and Defler 1996; Stevenson et al. 1998; Di Fiore 2004). Depending on resources, wild woolly monkeys are reported to spend large amounts of time preying on insects and small animals. Due to these predation habits being higher than many other new-world primates, the protein requirement for this species is of particular interest and may be lacking in many captive diets. While many researchers have followed woolly monkeys in the wild, no one has yet collected their naturally consumed diet items for complete laboratory nutritional analyses. Therefore, woolly monkey nutritional needs are poorly understood. However, due to their susceptibility to diseases typically associated with nutrition in captivity, it appears that woolly monkeys may be unique both with regard to their nutritional requirements and associated nutritional disorders.

In an attempt to ascertain some answers to the nutritional concerns surrounding the woolly monkey, several nutrition research projects were recently conducted. This research had two primary objectives. The first objective was to verify the theory that woolly monkeys do not thrive in captivity and if proven, to determine whether a nutritional cause for the primary disorders afflicting captive woolly monkeys could be isolated via historical research. The second primary objective was to investigate the effects that carbohydrates (particularly sugars) and lipids have on woolly monkey serum nutritional profiles, serum diabetic determinants, and stress hormone (cortisol) concentrations.

6.1.1 Woolly Monkey Historical Data Analysis

Written survey reports, International Species Information System (ISIS) historical record analysis, and woolly monkey-specific zoological studbook record analyses were studied to gather data on the survivability of the captive woolly monkey from 1990 to 2005. Data on spider monkey species also were collected from five representative institutions for comparative analysis. In the studied 16 years, the total woolly monkey population decreased by 11 %. The number of institutions holding woolly monkeys also decreased and the birth-to-death ratio was calculated to be below 1 (0.65) compared to that of the spider monkeys (1.26). Thus, one woolly monkey death was reported for every 0.65 births while 1.26 spider monkeys were born for each death. The low woolly monkey birth to death numbers were even more pronounced in the female population (0.47 births to each death vs. 0.74 for the males). The primary two causes of mortality in woolly monkeys within the records were infant and gestational failures to thrive (53 %) and cardiovascular events (15 %; Ange-van Heugten et al. 2010). Failures to thrive were defined as the infant dying of unknown causes before the age of 1 or the mother dying during gestation, delivery, or within a few weeks after delivery.

Only one institution managed to breed several generations of the woolly monkey. In addition, many of the successful offspring from this institution were transferred to other facilities where they were typically the successful monkeys. Thus, lack of genetic diversity in captive woolly monkeys may have a negative influence on their reproductive success since some lineages seem more successful than others. It is possible that genetic abnormalities in nutrient metabolism as well as overall unnatural diet nutrient composition are contributing factors for poor captive success noted in woolly monkeys.

6.1.2 Serum Chemistry

It was deemed important to study woolly monkey historical nutritional serum chemistry profiles to potentially isolate abnormalities and help with their health diagnostics. Serum chemistry medical analyses from 30 woolly monkeys housed at two of the primary institutions housing this species (Apenheul, The Netherlands, and The Louisville Zoo, USA) over a 12-year period were examined. The specific objectives for collecting this information were: (1) determine and publish baseline serum concentrations for captive woolly monkey comparisons; (2) compare serum concentration means by monkey gender, age groups, and captive holding institutions; (3) compare overall serum concentrations to the closest genetic relatives of the woolly monkey; and (4) isolate serum chemistry abnormalities that may affect captive woolly monkey life longevity (Ange-van Heugten et al. 2008a). Interestingly, serum chemistry means were similar to previously reported concentrations for howler (*Aloutta* sp.) and spider monkeys with the possible exception of alanine aminotransferase (ALT) and gamma-glutamyl transferase (GGT) concentrations being higher, while creatinine and phosphorus concentrations were lower. These abnormalities could be indicative of cardiovascular and liver disease noted in captive woolly monkeys.

Serum glucose (6.7 mmol/L) was above the baseline range when compared to human and spider monkey normals. These elevated glucose concentrations were of interest due to their potential type II diabetes link and this specific health concern has often been a rumored woolly monkey concern and reported in keeper log books, although seldom noted in veterinary records.

Alkaline phosphatase, ALT, and sodium (Na) were higher in females, and magnesium (Mg) was higher in males ($P<0.05$). Alkaline phosphatase, Mg, and phosphorus were highest ($P<0.05$) and calcium, Na, and ferritin tended to be highest ($P<0.10$) in the oldest animals. Albumin, alkaline phosphatase, chloride, Na, and total bilirubin were higher for one of the two animal housing facilities while GGT, glucose, and lactate dehydrogenase were lower ($P<0.05$). Health implications for these differences were not known.

Although potential abnormalities were noted, future research studies are needed to determine serum concentrations of a large population of free-ranging woolly monkeys to elucidate parameters that contain aberrant concentrations and potentially decrease the quality of health.

6.1.3 Diabetes

Due to the elevated glucose concentrations noted in the historical serum concentrations discussed previously, research was conducted to elucidate connections between captive woolly monkeys and diabetes. Blood and urine samples were collected from six captive woolly monkeys with known hypertension and related health problems during routine physical examinations to determine if type II diabetes and daily diet composition were the underlying links to their health problems. These monkeys had average blood pressure results via historical records that were significantly elevated (156 mm Hg) compared to human and primate reference ranges (120–140 mm Hg) despite daily consumption of several medications in an attempt to lower blood pressure (Ange-van Heugten et al. 2007).

Fasting concentrations of glucose (real-time indicator of insulin function), insulin (determinant of insulin insufficiencies), fructosamine (indicator of blood glucose control over the past 2 or 3 weeks), and glycated hemoglobin (indicator of long-term blood glucose status) were determined. Circulating lipids (high-density lipoprotein (HDL) cholesterol, low-density lipoprotein (LDL) cholesterol, total cholesterol, and triacylglycerides) also were evaluated as indicators for the potential risk of heart and vascular disease. Urine was collected and analyzed for glucose concentrations. Finally, diet disappearance was determined for 3 days prior to blood collection and nutrient content was calculated. Serum analyses were within normal ranges (fructosamine, 139–242 μmol/L; glucose, 2.2–4.8 mmol/L; glycated hemoglobin, 3.5–4.7 %; insulin, 6.2–13.0 μU/ml; triacylglycerides, 0.4–3.4 mmol/L; total cholesterol, 2.5–5.1 mmol/L; HDL cholesterol, 0.4–1.6 mmol/L; and LDL cholesterol, 1.8–3.4 mmol/L) when compared to new-world monkeys, old-world monkeys, and humans (Ange-van Heugten et al. 2007). Urine glucose concentrations were below detection limits. Diets were not limiting in starch and total sugars and were similar in non-starch polysaccharides. Potential dietary deficiencies were noted for vitamin A, vitamin D, calcium, phosphorus, and selenium (NRC 2003). However, the diet composition did not raise concerns as a causative factor associated with diabetes mellitus, glucose metabolism problems, or the diagnosed hypertension. Results indicated that diabetes mellitus is not a problem, at least within this sample of captive woolly monkeys. This study could not make any health observations regarding gestational diabetes and it should be noted that prescribed medications could have impacted data interpretation.

6.1.4 Fecal and Salivary Cortisol

It is well known that cortisol can be elevated by high-fat and high-sugar diets (Seematter et al. 2005) and therefore it has been hypothesized that woolly monkey stress and hypertension could be related to captive diet composition. Potential stressors, such as an unnatural diet, can reduce the success of rearing primates because chronic activation of an individual's stress response can have detrimental physiological effects on animal well-being. Thus, the objectives of the cortisol research projects were to investigate the impact of diet composition, particularly simple sugars, at multiple zoological institutions on fecal and salivary cortisol concentrations in woolly and spider monkeys.

6.2 Methods

Fecal (272) and salivary (66) samples from woolly ($n=27$) and spider monkeys ($n=61$) were collected from four US and three European zoos and were analyzed for cortisol concentrations (Ange-van Heugten et al. 2009). The zoos with the highest fecal cortisol concentrations also had the highest salivary cortisol ($P \leq 0.05$). For European zoos, fecal cortisol concentrations differed between zoos for both spider and woolly monkeys ($P \leq 0.05$) and surprisingly, spider monkey fecal cortisol concentrations were higher than those from woolly monkeys within the same zoos. This could be an indicator that stress is not a health factor for the successful longevity of these primates or could simply denote species-specific differences in cortisol measures between these two monkey species. Interestingly, within each cortisol study, the zoos with the highest dietary carbohydrates, total sugars, glucose, and dietary fruit content had the highest cortisol concentrations. This could be due to the fact that wild fruits have higher contents of fiber, minerals, protein, and vitamins and a lower content of total sugar and sucrose (having more fructose and glucose) than the cultivated fruits fed in captivity (Baker and Baker 1998; Milton 1999).

This is further validated by the fact that monkey cortisol concentrations were highest for the zoos that did not meet crude protein requirements and fed the lowest percentage of nutritionally complete primate feeds and crude fiber. Large dietary differences did exist among zoos with respect to the diets for their monkeys and therefore planning more universally standardized diets for both woolly and spider monkeys could be beneficial. The life span and reproductive success of captive primates could potentially improve if stressors and negative effects of nutrition on the health status are reduced and dietary nutrients are optimized. It should be noted that behavior, keeper interaction, visitor interaction, and housing differences likely also contributed to the cortisol differences noted in this research study. However, the dietary impact remains very intriguing.

6.2.1 Inulin-Type Fructans

Since previously discussed research indicated that high levels of dietary total carbohydrates, total calculated sugars, and glucose may increase cortisol concentrations in spider monkey and woolly monkey feces, it was hypothesized that adding dietary inulin-type fructans (ITF) to the diets may indirectly reduce stress responses in both woolly and spider monkeys. ITFs are considered prebiotics and are fermented in the gastrointestinal tract (GIT) and, as a result, physical and chemical conditions of the chyme (the fluid mass of partially digested food passed from the stomach to the first part of the small intestines) are changed. These changes include altered GIT microflora activity and changed gut immune functions (Roberfroid 1999; Roberfroid 2005; Verdonk et al. 2005). These ITF effects may be pertinent to the survival of captive woolly monkeys (*Lagothrix* ssp.) specifically by their potential to alleviate diabetes, hypertension, and indicators of stress while increasing reproductive and immune functions.

The objectives of this research study were to: (1) compare fecal cortisol levels in woolly and spider monkeys and establish normal fecal cortisol levels and (2) evaluate the effect of ITF supplementation in the daily diets of both woolly and spider monkeys, housed at the same institution, on fecal cortisol. A 3-day diet disappearance study was conducted and indicated that, in general, the diets consumed by woolly and spider monkeys at this institution met nutrient recommendations (NRC 2003; Ange-van Heugten et al. 2007). However, vitamin A concentrations (including β-carotene) were 10–30 times above recommendations. Due to the possibility of toxic effects of fat-soluble vitamins, this was a concern. Subsequently, ITF (containing 90–94 % inulin) was added to the daily diet for spider (*Ateles* sp.; $n=9$) and woolly monkeys ($n=7$), individually, at 5 g per day for 4 weeks. Fecal samples were collected prior to supplementation, after 2 weeks and after 4 weeks. Fecal cortisol concentrations were not significantly affected by ITF; however, fecal cortisol was numerically decreased after the 4-week ITF supplementation, primarily in spider monkeys (110 vs. 65 ng/g dry feces). It is interesting to note that spider monkeys showed higher fecal cortisol levels than woolly monkeys in the previous research as well. Since ITF supplementation tended to decrease fecal cortisol more in the spider monkeys than in the woolly monkeys, perhaps it could be argued that ITF supplementation worked better where it was needed most. The results from this study suggest that ITF supplementation may have positive effects on captive primate well-being via improving GIT health and therefore overall health when fed at higher dosages or when consumed for longer periods of time. However, additional research with larger populations of monkeys is recommended.

6.3 Discussion: Research Implications and New Diet Strategy

Many conservationists perceive the woolly monkey as a species that is too difficult to maintain in captivity. The exact causes of the problems in captive woolly monkey populations have, however, not been isolated. While research suggests that diabetes is not the primary problem affecting these monkeys, their captive diet is likely too high in total sugars (and the captive diet sugars likely do not reflect their wild diet). It is apparent that complete analyses of diets and serum nutrition parameters from wild monkeys are needed for comparisons to the captive parameters recently compiled. These comparisons could ensure that captive diets are as similar as possible to those of free-ranging animals.

Recent nutrition research further indicates that supplementation with prebiotics (such as ITF) may have beneficial effects on exotic animal health. Thus, future nutrition research with safe dietary supplements should be continued.

Regardless of the insights made into the nutritional issues facing the woolly monkeys, numerous new questions and areas for needed research have been unearthed. The most critical area of nutritional research needed for the woolly monkey is information about the diets of wild animals to obtain information for comparative analyses. It is also critical to better understand the genetic makeup of the woolly monkey captive population compared to that of wild animals. This is due to the potential for inbreeding within a very small captive population and the fact that it appears that some woolly monkey family lines are able to breed while others are not. Genetic analyses compared with nutrition and reproduction histories could provide important information for this species. Nutritional disease-related problems within this species are genetic in nature. Therefore, it is recommended to conduct future research to determine whether woolly monkeys with the highest fecal cortisol concentrations have lower life expectancies and reproductive rates, and to examine captive versus wild diet and genetics differences.

Preserving exotic species in captivity and in the wild are imperative to ensuring the ecological diversity upon which we are accustomed. With each species that goes extinct, future species (plant and animal) are in increased jeopardy. Preservation of many of these species, such as the woolly monkey, cannot happen without the joint scientific efforts of researchers within the nutrition community. While exotic animal research is challenging, developing a trusting relationship with animal care givers and formulating noninvasive research techniques can gleam diagnostic and preventative answers for factors that cause negative animal well-being. Zoos and concerned primate keepers have tried various methods to reduce stressors and health problems within captive woolly monkey populations. These methods include medications, removing the woolly monkeys from public exhibits, altering feeding schedules to deliver sugar loads gradually, altering diet items to perceived natural foods, and stopping breeding. However, cortisol measures have not been taken before and after the removal of these potential stressors and, therefore, little is known about the success of such techniques.

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Chapter 7
Effect of Housing Conditions and Diet on the Behavior of Captive Woolly Monkeys (*Lagothrix*)

Diana Carolina Guzmán-Caro and Pablo R. Stevenson

Abstract The frequent capture of wild individuals and illegal pet trade of woolly monkeys has become one of the main threats for this species in Colombia. As a consequence, these primates frequently arrive at captive centers and zoos, and in captivity they show a high mortality. Finding conditions that promote the expression of natural behaviors in captive animals is considered beneficial for their physical and psychological well-being and a key step in rehabilitation and reintroduction programs. This study evaluates the effect of housing conditions and diet on the behavior of captive woolly monkeys in Colombia. Behaviors were quantified using focal animal sampling and instantaneous records. Comparisons were made to wild behavior patterns. Housing conditions were evaluated in terms of volume, density, and environmental enrichment; and diet was evaluated in terms of consumption quantity, type, and nutrient composition. Results show that enclosures with a larger size and a higher level of environmental enrichment are associated with more natural behavior patterns. Results also suggest that food and nutrient deprivation may have a considerable negative effect on behavior. This study provides valuable knowledge for the conservation of captive woolly monkeys. Results from this study should be implemented into captive well-being and the development of rehabilitation and reintroduction programs for woolly monkeys.

Keywords Captive diet · Captive primates · Environmental enrichment · Housing conditions · Illegal trade · Rehabilitation · Woolly monkeys

7.1 Introduction

Illegal wildlife trade is one of the main threats to primate species in Colombia (Hernandez-Camacho and Cooper 1976; Gómez 2000; Defler 2004, IUCN 2008). Primates are particularly attractive as pets and as laboratory animals (Mancera and

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D. C. Guzmán-Caro (✉) · P. R. Stevenson
Universidad de Los Andes, Bogotá, Colombia
e-mail: guzman@asoprimatologicacolombiana.org

P. R. Stevenson
e-mail: pstevens@uniandes.edu.co

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Reyes 2008) and, consequently, large numbers of individuals from different species are constantly captured and removed from their natural habitat (Gómez 2000; Defler 2004). Many of the captured or traded individuals are subsequently confiscated by authorities or voluntarily offered, and sent to or received by centers of wild animal management or zoos, where they usually spend the rest of their lives in captivity. However, the increasing number of captive individuals, the low number of captive centers and zoos in the country, and problems such as lack of space and resources, among others, make it difficult for these centers to provide adequate conditions for captive primates or even accept new individuals (Echeverry, Millan, personal communication).

Illegal trade has thus become a main issue for primate conservation in Colombia that needs to be urgently addressed. The development of breeding, rehabilitation, and reintroduction programs for captive primates is a valuable conservation strategy that urgently needs to be expanded in Colombia. However, few studies have been performed on captive primates in Colombia (Stevenson et al. 2010), and the lack of information on how the species respond to different captive conditions has restrained the development of conservation plans involving captive individuals (but see: Price 1992; Ortíz and Stevenson 2003; Peres 2005).

Providing captive animals with conditions that promote the performance and maintenance of natural behaviors is considered beneficial for captive animals' welfare (i.e., the psychological and physical well-being of animals) and a key step in rehabilitation and reintroduction programs (Redshaw and Mallinson 1991; Shepherdson 1994; Shepherdson et al. 1998; Mellen and Sevenich 2001; Custance et al. 2002; Little and Sommer 2002; Hosey 2005; Seddon et al. 2007; Laule and Whittaker 2007). Environmental enrichment (EE) techniques, in which individuals are exposed to a more naturalistic environment, have been suggested as an adequate approach to stimulate species-typical behaviors in captive primates (Snowdon 1994; Schapiro and Lambeth 2007). However, enrichment methods should be based on adequate knowledge of the species' natural habitat (i.e., functional attributes such as physical complexity and vegetation), and on how individuals interact with it (i.e., patterns of habitat use; Little and Sommer 2002; Hosey 2005). Furthermore, the effectiveness of these techniques in promoting the display of natural behaviors should be evaluated through wild–captive comparisons (Redshaw and Mallinson 1991; Renner et al. 2000; Little and Sommer 2002; Hosey 2005); thus, complete information on the species' natural history and behavior patterns is also required.

Captive primates are usually provided diets that differ greatly from natural diets (Crissey and Pribyl 1997; Hosey 2005). Inadequate diets are often associated with health problems (e.g., nutrient deficiency and obesity) in captive individuals, and may also have negative effects on behavior (Hosey 2005). Providing captive primates with diets similar to the ones they consume in their natural habitats has been proposed as an adequate feeding strategy (Crissey and Pribyl 1997). However, the lack of information on the nutritional composition of their natural diet has made it difficult to determine the proper captive diet. Furthermore, differences in feeding strategies, gut morphology, and nutrient requirements among species indicate that captive feeding approaches must be species specific (Crissey and Pribyl 1997).

Woolly monkeys (*Lagothrix*) represent one of the most widely distributed genera in Colombia (Stevenson et al. 2010), and they have been found to be valuable seed dispersers in Neotropical forests (Stevenson 2000). In Colombia, these valuable monkeys face many threats. Wild populations of woolly monkeys are decreasing because of habitat destruction due to different processes of human expansion in most of the regions they inhabit, as well as hunting, both legal and illegal (Etter and van Wyngarden 2000; Stevenson et al. 2010). These monkeys' large body size not only makes them easy targets for hunters but also a preferred food item for indigenous people (Peres and Palacios 2007). Also, together with *Saimiri, Saguinus,* and *Cebus,* they are particularly threatened by illegal trade due to their popularity as pets and, as a consequence, they frequently arrive at zoos and captive centers (Echeverry, personal communication). Unfortunately, woolly monkeys are threatened in captivity as well, since *ex situ* populations typically sustain high mortality and low breeding success (Debyser 1995; Ange-van Heugten et al. 2008). Studies on captive woolly monkeys have suggested that the leading causes of woolly monkey deaths are related to hypertension complications and undetermined factors during the first year of life (Debyser 1995; Ange-van Heugten et al. 2008, this volume). An inadequate diet has been proposed as a probable cause of health problems, but the link between nutritional problems and mortality has not been identified (Ange-van Heugten et al. 2007). Lastly, the influence of housing conditions and diet on the behavior of captive woolly monkeys has been poorly studied.

This study evaluates how different housing conditions and captive diets affect woolly monkeys' behavior at different zoos and captive centers in Colombia. Through the assessment of behavioral patterns, we determined to what extent the (1) enclosure size, density of individuals within enclosures, and EE and (2) the quantity and composition of the diet affect captive woolly monkeys' behavior. We used the same methods applied for in situ studies to make direct comparisons between captive and wild behavior patterns. Finally, we identified which housing conditions and captive diets seem to be associated with more natural behavior patterns in captive woolly monkeys. This information will be used to propose a preliminary protocol of animal management that establishes which captive conditions should be met to promote improved expression of natural behaviors in captive woolly monkeys. However, the effectiveness of this protocol for promoting natural behavior patterns in these primates should be evaluated experimentally.

7.2 Methods

7.2.1 Study Sites

Our study sites included nine locations with captive woolly monkeys within Colombia (Table 7.1). Data on woolly monkeys' behavior, housing conditions, and captive diet were collected between December 2010 and September 2011 on all woolly

Table 7.1. Type and location of the different study sites

Study site	Type	Location (Department)
Zoológico Santa Cruz	Zoo	Cundinamarca
Zoológico de Piscilago	Zoo	Tolima
Zoológico Jaime Duque	Zoo	Cundinamarca
Zoológico de Cali	Zoo	Valle
Bioparque los Ocarros	Zoo	Meta
Zoológico de Barranquilla	Zoo	Atlántico
Zoológico Cafám	Zoo	Tolima
Fundación El Refugio	Nonprofit organization	Valle
Centro de Atención y Valoración Cortolima	Attention Center for Wild Animals	Tolima

monkey enclosures present at each site. A total of 29 *Lagothrix* individuals and a total of 14 enclosures were sampled (Table 7.2).

7.2.2 Behavior in Captivity

The behavior of all *Lagothrix* individuals present in each enclosure was evaluated through focal sampling methods. Instantaneous samples were taken every 10 min between 0600 and 1800 h for 5 days, per individual. For each instantaneous sample, the following information was collected:

1. Type of activity, using the same categories used by studies on wild woolly monkey populations (Stevenson 2006; González and Stevenson 2010; Zárate 2009; Vargas-Troncoso 2011): (a) feeding, (b) moving, (c) resting, and (d) social interactions (i.e., play, social grooming, mating, or aggression).
2. When the observed activity was feeding, the consumed item was identified and classified according to categories used by previous studies on wild woolly monkey populations (more information on these categories is available in the Captive Diet section below).

7.2.3 Housing Conditions

Housing conditions were studied for all woolly monkey enclosures using three variables: (1) enclosure size, (2) density of individuals in the enclosure, and (3) index of EE, measured as follows:

1. *Enclosure size:* Volume of space in which individuals are kept (in cubic meters).
2. *Density of individuals:* Number of individuals per cubic meter.
3. *Index of EE:* Two EE indexes were constructed using information on surface areas for different types of substrates, weighted by the degree of similarity to substrates used by wild woolly monkeys. Indexes were based on the assumption

Table 7.2. Information on the individuals found in each of the studied enclosures at the different study sites

Study site	Enclosure	Individual	Age–sex class
Zoológico Santa Cruz	SC	Niña	Adult female
		Margarita	Adult female
Zoológico de Piscilago	PL	Calimeño	Adult male
		Juliana	Adult female
		Paulo	Sub-adult male
		Chepe	Sub-adult male
Zoológico Jaime Duque	JD	Pocho	Adult male
		Isabella	Adult female
		Carolina	Sub-adult female
Zoológico de Cali	CA1	Rosita	Adult female
		Margara	Adult female
	CA2	Negro	Sub-adult male
	CA3	Jazmin	Female juvenile
	CA4	Petunia	Adult female
		Acacio	Adult male
	CA5	Rubus	Adult male
Bioparque Los Ocarros	OC	Niño	Adult male
		Paquita	Adult female
		Lina	Adult female
		Tommy	Sub-adult male
Zoológico de Barranquilla	BA	Dave	Adult male
		Mariana	Adult female
		Manu	Female juvenile
Zoológico Cafám	CF	Olivia	Adult female
		Popeye	Adult male
Fundación El Refugio	ER	Manuela	Adult female
Centro de Atención y Valoración Cortolima	CT1	Hembra	Adult female
		Ñato	Adult male
	CT2	Matilde	Sub-adult female

that a complex environment in terms of structure may favor the expression of natural behaviors. Structural complexity was measured in terms of the area of potential supporting structures. However, since different structures are used in different ways by wild woolly monkeys, two criteria were used to weigh the importance of different substrates: diameter and height.

The first index was based only on information on the diameter of the substrates used for moving by the woolly monkeys in Yasuní National Park, Ecuador (Cant et al. 2001). Thus, since woolly monkeys move on substrates of less than 2 cm in diameter 15 % of the time, the total area of that type of objects was weighted by this proportion (i.e., multiplied by 0.15). Similarly, substrates between 2 and 5 cm in diameter were used 22 % of the time; therefore, the weighted area of that type of substrate was obtained by multiplying the total available area by 0.22 to obtain the relative contribution. The different diameter categories were weighted using the same procedure. Flat surfaces were included in the >20 cm category, which represents substrates that are rarely used by wild woolly monkeys (4 % of the time). The area of diagonal substrates was included without correction, but the area of vertical ropes was estimated as if the monkeys were able to use them at an angle of 45°. The area of large trunks (>40 cm in diameter) was included just as the basal area.

The second index also included the substrate type in the same way described above, but it also included height as an additional weighting variable. For this purpose, we used the patterns of vertical stratification described from woolly monkeys in Tinigua Park, Colombia (Stevenson and Quiñones 1993). In natural conditions, woolly monkeys prefer the lower levels of the canopy, avoid the forest floor, and only use emergent trees occasionally for feeding purposes. This pattern has been explained as a behavioral preference to avoid predation, which may not be too relevant for captive animals, unless they are in a process of rehabilitation for reintroduction. Then, the second index considered the height at which the surfaces were found (i.e., forest floor: 0.1 %, >0–3 m: 3 %, 3–6 m: 12.9 %, 6–9 m: 18.8 %, 9–12 m: 25.5 %, 12–15 m: 19.8 %, 15–18 m: 9.9 %, 18–21 m: 5.0 %, 21–24 m: 3 %, 24–28 m: 1 %, >28 m: 0.8 %). Both indexes were finally obtained by adding all weighted areas and dividing the total value by the number of individuals that are potentially using those substrates (m^2 per capita). Information on how to calculate these indexes may be provided by the authors upon request.

7.2.4 *Captive Diet*

Consumption Times

Data on all food items consumed by individuals from 0600 to 1800 h were collected for 5 days per enclosure. Items were individually identified, and the time spent by individuals consuming each item was registered for each feeding event. These data were collected for a maximum of two individuals per day; therefore, for enclosures with more than two individuals, the total number of sampling days per individual was less than 5 (all individuals were sampled for a minimum of 2 days). For comparative purposes, food items were classified according to categories used to study the diet of wild populations (Stevenson 2006; Gonzalez and Stevenson 2010; Zárate 2009; Vargas-Troncoso 2011): (1) fruits, (2) leaves (classified as vegetables in this study), (3) seeds and unripe fruits, (4) flowers (including vegetables such as cauliflower and broccoli), and (5) others (including dairy products, eggs, meats, cereals, bread, cakes, cookies, chips, dog-food, soil, baby-food, marmalade, icecream, and small reptiles).

Consumption Quantities

Data on the type and quantity (in grams) of food items offered daily to *Lagothrix* individuals per enclosure were collected based on information provided at each site. Additionally, information on the composition (i.e., number and type of items provided) and time of all feeding bouts (i.e., when individuals were provided a particular diet) was collected for 5 days per enclosure. To estimate consumption values for the different items provided, we weighed the remaining items or pieces per day, or per feeding bout when possible. In a few cases, we were only able to weigh the remaining items or pieces for a limited number of days.

Total Daily Consumption

Consumption rates (g/s) for all consumed food items were estimated per enclosure, based on information on daily consumed quantities and daily consumption times. For items for which consumed quantities were unknown, feeding rates of similar items were used. Daily consumed quantities for each item per enclosure were estimated using the calculated consumption rates and daily consumption times.

Nutrient Composition and Consumption

Nutrient composition for the consumed food items was studied as grams of (1) crude fiber, (2) total sugars, (3) crude protein, and (4) crude fat, per gram of food. For each particular type of item ($n=77$), nutrient composition was estimated using databases from Zootrition software (Wildlife Conservation Society 1999) and the online USDA National Nutrient Database for Standard Reference (USDA Agricultural Research Service 2011). When this information was not available for a particular item ($n=10$), the nutrient composition of the most similar item found in the databases was used. Daily nutrient consumption values were estimated using information on nutrient composition and daily consumed quantities for each item.

7.2.5 Data Analyses

Activity and Feeding Behavior Patterns

We estimated the frequency of instantaneous samples on each activity and diet category for each observed individual per day. These frequencies were used as sampling units for further analyses. In order to assess differences between the activity budgets and diet composition, we calculated Chi^2 values by comparing the observed values in captive individuals and the expected frequencies from an average obtained from data on studied wild populations (Stevenson 2006; Zárate 2009; Gonzalez and Stevenson 2010; Vargas-Troncoso 2011). To estimate differences in activity budgets, we included the frequencies for feeding, movement, and resting, but we excluded social interactions. This approach is justified by the fact that increased rates of social interactions do not always represent unnatural behaviors (i.e., more grooming or play events). To compare feeding behavior patterns between captive and wild woolly monkeys, Chi^2 analyses were performed based on calculated frequencies for the different food categories (fruits, vegetables, seeds and unripe fruits, arthropods, and other items). Expected frequencies were calculated using reported activity and diet percentages for wild woolly monkey populations (Stevenson 2006; Zárate 2009; Gonzalez and Stevenson 2010; Vargas-Troncoso 2011). Chi^2 values were calculated per individual and per enclosure.

Effect of Housing Conditions and Diet on Activity Behavior Patterns

Logarithmic or linear regression analyses (depending on best-fit line) were performed on SPSS software (SPSS Inc. 2006) to evaluate the effect of housing conditions (enclosure volume, density of individuals, and EE indexes) and diet (total consumption and crude fiber, total sugars, crude protein, and crude fat consumption) on the activity Chi^2 value obtained for the different enclosures. Data on volume, the two EE indexes, crude fiber, and crude fat were transformed using the Ln function to obtain a normal distribution.

Effect of Diet on Feeding Behavior Patterns

Given the nonparametric distribution of feeding behavior Chi^2 data, Spearman correlation analyses were performed using SPSS software (SPSS Inc. 2006) to evaluate the relationship between diet (quantity of crude fiber, total sugars, crude protein, and crude fat) and feeding behavior patterns.

Estimation of Adequate Captive Conditions

Minimum values for *adequate* housing conditions and diet (i.e., minimum values that are expected to favor the expression of natural behaviors) were estimated using linear equations from regression analyses between Chi^2 values and the different variables. These values were not estimated for density and crude fiber, since these variables did not show a clear relationship with activity Chi^2 values. Minimum values were estimated as ranges of minimum values, using the highest non-significant activity Chi^2 value to calculate the upper limit, and the lowest significant activity Chi^2 value to calculate the lower limit.

7.3 Results

Woolly monkeys within the same enclosure tend to show similar activity patterns. However, in 4 out of 14 enclosures, individuals showed significant differences in the percentage of time spent feeding. Significant differences between or among

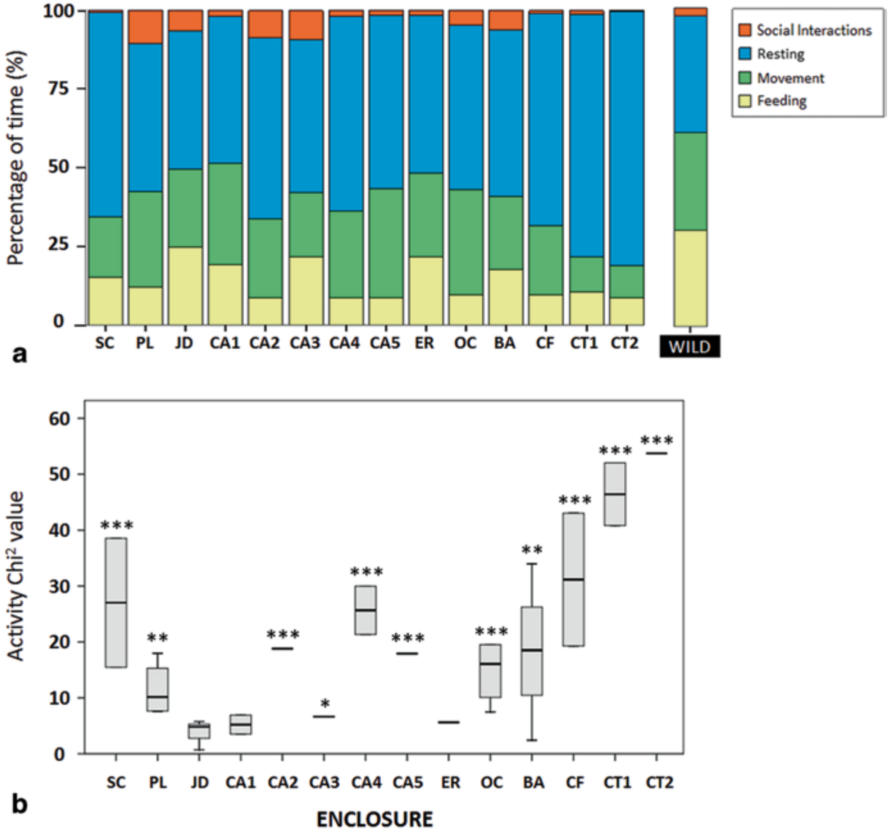


Fig. 7.1 **a** Percentage of time spent by woolly monkeys on the different activities at the different enclosures (*SC* Santa Cruz, *PL* Piscilago, *JD* Jaime Duque, *CA* Cali, *ER* El Refugio, *OC* Ocarros, *BA* Barranquilla, *CF* Cafám, *CT* Cortolima) and in the wild and **b** activity Chi^2 values for the different enclosures. *Boxes* show data distribution from enclosures with more than one individual

individuals were also found in five enclosures for movement, and in three for resting and social interactions (Appendix 7.1). The percentage of time spent by woolly monkeys in the different activities also varied among enclosures and between captive and wild environments (Fig. 7.1a). In general, captive woolly monkeys spend more time resting and less time feeding compared to wild woolly monkeys. However, Chi^2 analyses indicate that the activity behavior patterns found for three of the studied enclosures are not significantly different from patterns found for wild populations (JD, $p=0.272$; CA1, $p=0.082$; ER, $p=0.058$; Fig. 7.1b).

The percentage of time spent by woolly monkeys feeding on the different types of items varies greatly among enclosures and between captive and wild environments (Fig. 7.2b). Accordingly, Chi^2 values for feeding behavior patterns show that, for all enclosures, the time spent by woolly monkeys consuming fruits, vegetables, seeds and unripe fruits, arthropods, flowers, and other items differs significant-

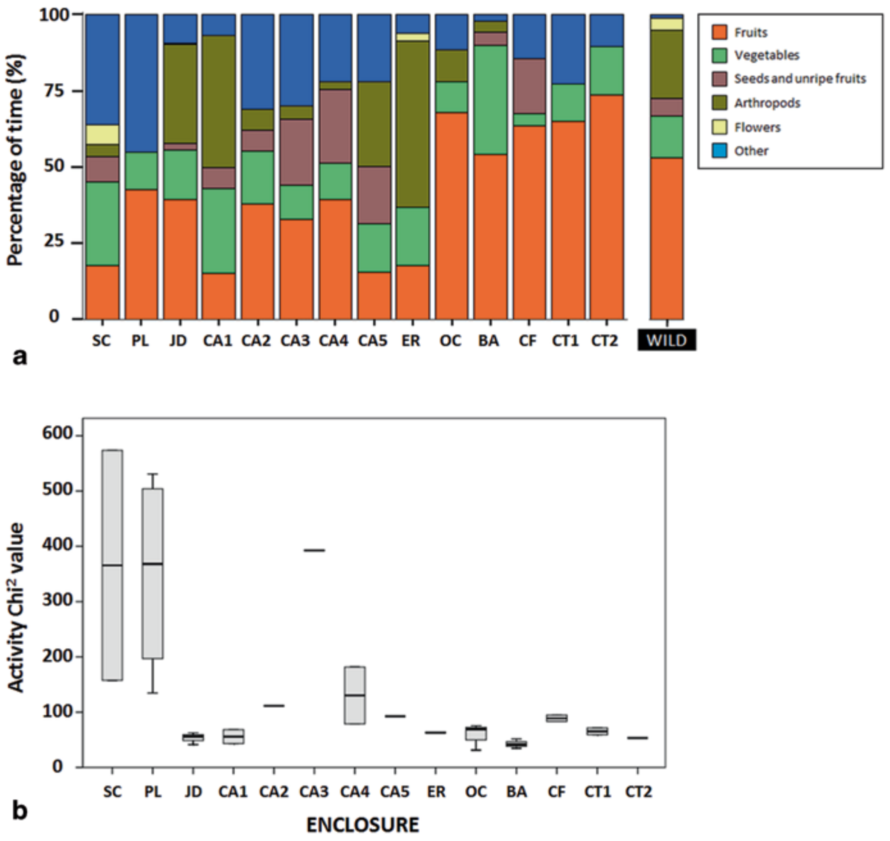


Fig. 7.2 **a** Percentage of time spent by woolly monkeys feeding on the different items at the different enclosures and in the wild and **b** feeding behavior Chi^2 values for the different enclosures. *Boxes* show data distribution from enclosures with more than one individual

ly from the feeding behavior patterns found for wild woolly monkeys ($p < 0.05$; Fig. 7.2b). Within this wide variation of feeding patterns, results show a tendency towards a higher consumption of *other* items and a lower consumption of fruits in captive woolly monkeys compared to wild populations.

Total daily food consumption per individual varies among enclosures both in terms of time (Fig. 7.3a) and quantity (Fig. 7.3c). Differences are also observed in the consumption time and quantity for the different item categories (Fig. 7.3b, d). However, the Pearson correlation analysis between total consumption time and quantity did not show a significant relationship (Pearson coefficient $=0.412$, $p=0.143$). Therefore, there is considerable variation in consumption rates among enclosures.

Regression analyses between activity Chi^2 values and housing conditions show a tendency towards more natural behavior patterns (lower Chi^2 values) in enclosures with a larger volume of space, lower density of individuals, and higher EE index

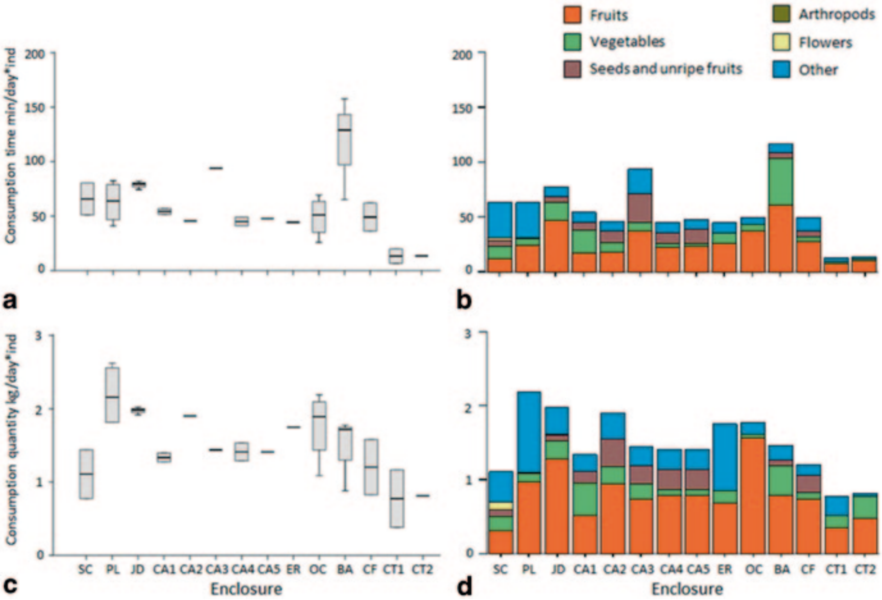


Fig. 7.3 Total consumption of food by captive woolly monkeys in different enclosures, in terms of **a** time and **b** quantity. The colored panels show consumption for the different food categories consumed, in terms of **c** time and **d** quantity, per individual per day. *Boxes* in (**a**) and (**b**) show data distribution from enclosures with more than one individual

values (Fig. 7.4). The logarithmic relationship between Chi^2 values and the two EE indexes was highly significant (Fig. 7.4c, d); therefore, EE seems to have a strong influence on captive woolly monkeys' behavior. Even though the relationship between activity Chi^2 values and enclosure volume was not statistically significant (Fig. 7.4a), the results suggest that this variable can have an important effect on captive woolly monkeys' behavior. On the other hand, although high densities within enclosures seem to have a negative effect on behavior (Fig. 7.4b), this relationship does not show a clear pattern.

Regarding diet variables, results from the regression analyses indicate that captive woolly monkeys tend to display more natural behavior patterns when they consume larger quantities of food and nutrients. The logarithmic relationship between activity Chi^2 values and total food consumption was highly significant (Fig. 7.5). Similarly, the logarithmic relationships between activity Chi^2 values and daily consumption of total sugars, crude protein, and crude fat also show statistically significant patterns (Fig. 7.6b–d). Crude fiber consumption did not show a significant relationship with activity Chi^2 values (Fig. 7.6a). On the other hand, Spearman correlation analyses between nutrient consumption and feeding behavior Chi^2 values indicate that none of the diet variables seems to be related to more natural feeding behavior patterns.

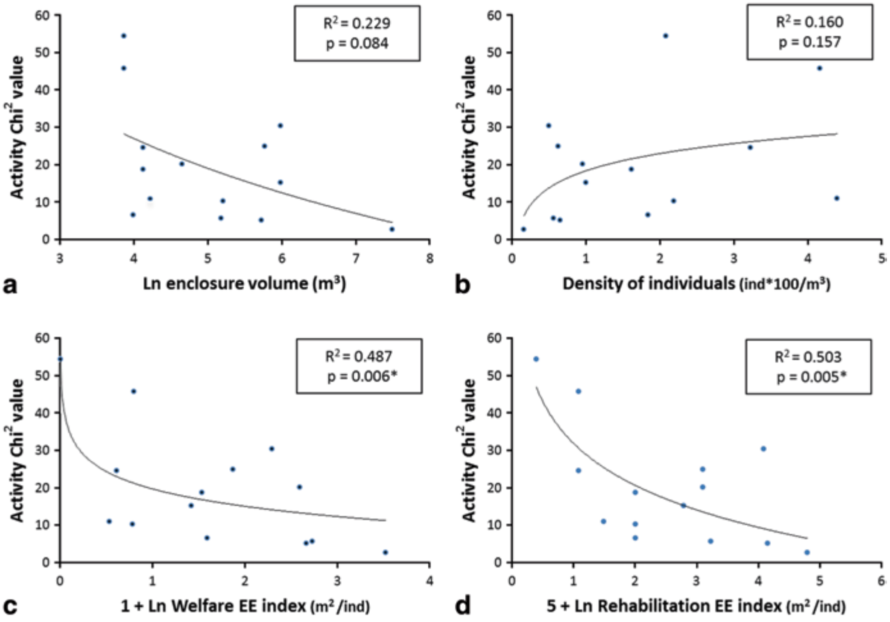
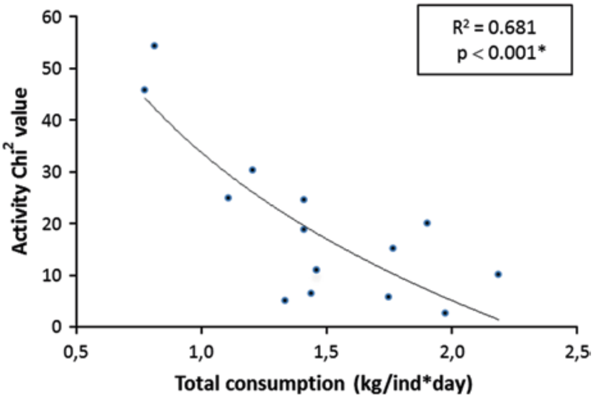


Fig. 7.4 Logarithmic regressions between Chi^2 values and **a** enclosure volume, **b** density of individuals, **c** welfare, and **d** rehabilitation EE indexes

Fig. 7.5 Logarithmic regression between activity Chi^2 values and total food consumption



Estimated ranges of minimum values for enclosure volume, EE indexes, total consumption, and sugars, protein, and fat consumption required to provide woolly monkeys with *adequate* captive conditions (i.e., housing conditions and diet that are expected to promote the display of natural behaviors) are shown in Table 7.3. The actual minimum value for each variable is expected to lie within the estimated minimum ranges. Even though these ranges were estimated using linear equations, the regression analyses indicate that the relationship between the activity Chi^2 values and these variables is best represented by a logarithmic model. Therefore, it is expected that variable values above the estimated minimum ranges will represent

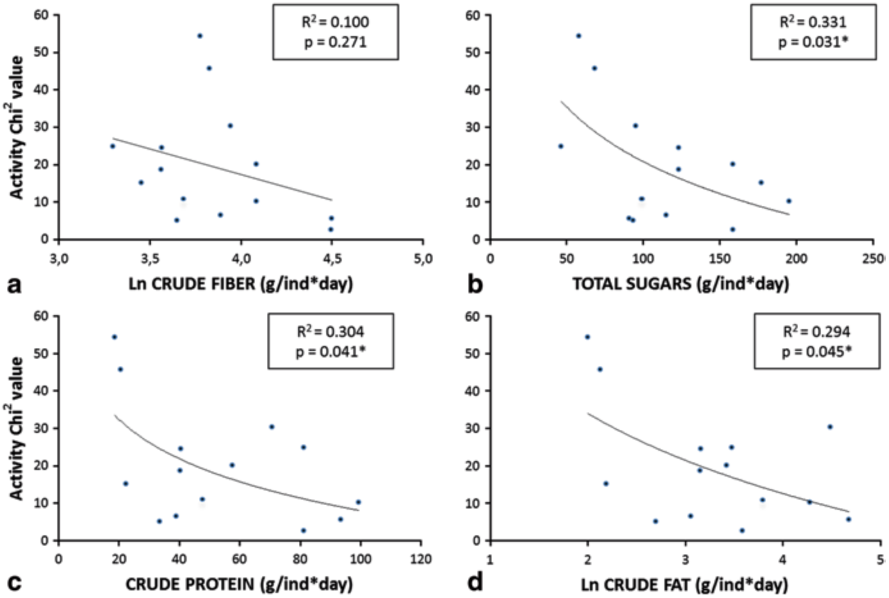


Fig. 7.6 Linear regression between activity Chi^2 values and **a** crude fiber; and logarithmic regressions between activity Chi^2 values and **b** total sugars, **c** crude protein, and **d** crude fat

Table 7.3 Minimum values for the different housing conditions and diet variables, required to provide captive woolly monkeys with *adequate* housing conditions and diet. The actual minimum value for each variable is expected to lie within the shown ranges

	Variable		Minimum range
Housing conditions	Enclosure volume *(m^3)*		1,103.81–1,250.10
	Environmental enrichment *(m^2/ind)*	Welfare Index	9.03–9.94
		Rehabilitation Index	0.80–0.84
Diet	Total consumption *(kg/ind.day)*		1.93–1.96
	Total sugars *(g/ind.day)*		186.88–191.41
	Crude protein *(g/ind.day)*		106.15–103.04
	Crude fat *(g/ind.day)*		118.10–129.50

an improvement in captive conditions until an undetermined stabilizing point is reached (i.e., when an increase in the variable values will not represent a further decrease in the Chi^2 value).

7.4 Discussion

In their natural habitat, woolly monkeys usually have large home ranges (Defler 1996; Stevenson 2006) and show behavior patterns dominated by feeding or foraging activities and movement (Di Fiore 2003; Stevenson 2006). Contrastingly, when captive, woolly monkeys are largely limited in terms of space and, since most of the food they consume is provided, foraging activities are greatly reduced. Accordingly, the activity percentages obtained for resting and feeding in the different enclosures were always higher and lower, respectively, compared to percentages reported for wild populations (Fig. 7.1a). However, some enclosures showed similar and even higher movement percentages than wild populations, suggesting that movement activities may not be strongly impaired under certain captive conditions. Overall, 11 out of the 14 studied enclosures showed activity budgets that were significantly different from natural patterns, corroborating the prediction that captivity negatively affects woolly monkeys' behavior patterns. Nevertheless, the remaining three enclosures indicate that natural activity patterns can be achieved in captivity and, therefore, this suggests that there are certain captive conditions that enable woolly monkeys to behave naturally in terms of activity budgets.

Captivity usually limits both the diversity and total area of substrates available for individuals to develop natural behavior patterns. The natural habitat of woolly monkeys consists of dense forest vegetation that provides them with a wide range of substrates that can be exploited in numerous ways (i.e., complex patterns of habitat use; Cant et al. 2001). Consequently, the absence of adequate substrates (i.e., similar to substrates used by wild woolly monkeys) may reduce activities such as foraging, and might also prevent individuals from expressing natural locomotor and postural behavior, among others. The significant association found in the regression analyses between the activity Chi^2 values and the two EE indexes supports these predictions. Low EE indexes, indicative of a lower availability of substrates similar to the ones used by wild woolly monkeys, were associated with less natural activity patterns, while higher EE index values were associated with more natural activity patterns (Fig. 7.3). These results therefore indicate that EE has a particularly important effect on behavior, and that substrate-deficient enclosures may hinder the expression of natural behaviors by limiting the range of activities that individuals are able to perform. Additionally, since the EE indexes reflect the degree of similarity with the natural habitat, these results also support the idea that more naturalistic environments help promote the expression of natural behaviors.

Enclosure size had a minor but still considerable effect on captive woolly monkeys' behavior. Individuals in larger enclosures tend to show more natural activity patterns, which once again suggests that space limitation has a negative effect on woolly monkeys' behavior, most likely by causing a reduction in movement. Finally, even though there is a slight tendency towards more natural behaviors in less dense enclosures, woolly monkeys are group-living animals and, therefore, solitary individuals may show abnormal behavior patterns due to the absence of social interactions. Still, captive woolly monkeys live in densities that are far higher than densities reported for wild populations (Stevenson 2007, 2011) and, therefore, this may also have a negative effect on behavior patterns.

Captive diets are rarely similar to natural diets (Crissey and Pribyl 1997; Hosey 2005), and this is also the case for captive woolly monkeys in Colombia, as shown by the results of the Chi^2 analyses (Fig. 7.2b). Wild woolly monkey populations can feed on fruits of approximately 200 species and plant material from at least 1,000 plant species (Stevenson 2004) and, while the number of potential arthropod species preyed on by woolly monkeys has not been quantified, it might be on the order of thousands in natural forests. Under captive conditions, the opportunity of a diverse diet is greatly reduced. Moreover, while feeding behavior in wild woolly monkeys is usually determined by food availability and preference (Stevenson 2004), in captive woolly monkeys it is mostly determined by food availability, and preference plays a minor role in an individual's feeding decisions. In most enclosures, little or no remaining items or pieces were left; thus, the proportions in which captive individuals consume items of the different categories mostly reflect the proportions in which these items were offered at the different study sites. Even though preference was observed in terms of the order in which the different items were consumed, this did not affect the final consumption proportions obtained for the different food categories. We also noticed that captive woolly monkeys were much less selective in leaf consumption. For instance, the consumption of mature leaves is rare in natural conditions (Stevenson 2006), but many of the studied individuals were observed eating dead leaves of several species that have been not reported in the diet of wild populations (i.e., *Cedrela montana*; Meliaceae).

In general, individuals that consumed larger quantities of food and main nutrients showed more natural activity patterns (Figs. 7.5 and 7.6). This could be related to caloric intake and energy budgets, since in some study sites, the total amount of food provided to individuals may not satisfy the basic caloric and nutritional requirements of the individuals. As a result, nutritionally deficient diets may cause abnormal behavior patterns, such as disproportionately large resting percentages, due to the lack of energy to perform other activities (i.e., movement). Nevertheless, these results have to be interpreted carefully since high sugar and fat consumption has been proposed as a probable cause of health problems in captive woolly monkeys (i.e., hypertension, diabetes; Ange-van Heugten et al. 2008). Therefore, although these results suggest that nutrient deprivation may negatively affect activity patterns in captive woolly monkeys, an excess of food should not be regarded as positive until the effects of diet on health problems and survivability are clarified.

This study suggests that both housing conditions and diet can have strong effects on captive woolly monkeys' behavior. Enclosures with a larger volume of space and a higher availability of substrates similar to the ones used by wild woolly monkeys seem to help promote the display of natural behavior in captive individuals. Thus, this study supports the prediction that housing conditions are crucial for the maintenance of natural activity patterns in captive woolly monkeys, and that more naturalistic environments are beneficial for captive individuals. On the other hand, providing captive woolly monkeys with a diet that satisfies the basic caloric intake and nutrient requirements of individuals is of great importance for individuals to be able to perform natural behaviors. Minimum values for *adequate* housing conditions and diet variables are proposed (Table 7.3). We suggest that in order to promote the expression of natural behaviors in captive individuals, or for the future development of rehabilitation programs, these values should be considered.

7.4.1 Post-Project Follow-up

Results from this study will be used to propose a preliminary protocol of animal management that lists favorable enclosure conditions and diet for the maintenance and rehabilitation of woolly monkeys in captivity. This protocol will be shared with all the participating institutions to encourage its implementation. With this document, institutions will be able to provide woolly monkeys with improved captivity conditions that might promote the maintenance of the natural behaviors. However, for a proper evaluation of the protocol's effectiveness, we intend to develop an experimental study to test whether individuals subjected to the suggested housing conditions and captive diet do, in fact, exhibit a more natural behavior, compared to individuals subjected to conditions indicated as being non-adequate. If the effectiveness of the protocol is confirmed, this would lead the way to the planning and construction of reintroduction projects for the species and, therefore, it would represent a valuable opportunity for conservation efforts.

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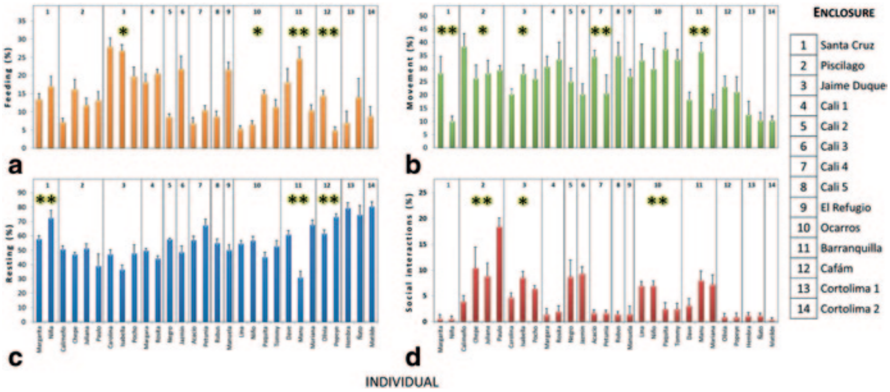
Appendix 7.1



Appendix 1. The figure shows activity budgets in terms of percentage of instantaneous records corresponding to **a** feeding, **b** movement, **c** resting, and **d** social interactions per individual. *Bars* show intraindividual variation. *Dotted lines* indicate group individuals present in the same enclosure. *Asterisks* indicate significant or highly significant statistical differences between activity budgets for individuals within the same enclosure

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Part IV
In Situ Ecology and Behavior

Chapter 8
Life History, Behavior, and Development of Wild Immature Lowland Woolly Monkeys (*Lagothrix poeppigii*) in Amazonian Ecuador

Christopher A. Schmitt and Anthony Di Fiore

Abstract Primate life histories are marked by remarkably long prereproductive periods, particularly in atelins. Woolly monkeys have among the longest immature phases relative to their body size, but the behavior of woolly monkey juveniles and adolescents has until now been largely unknown. This chapter establishes guidelines for identifying developmental landmarks in immature woolly monkeys and presents data on a study of the behavioral development and life history of wild juvenile and adolescent lowland woolly monkeys (*Lagothrix poeppigii*) in Amazonian Ecuador. Despite overall low levels of sociality across all ages in this taxon, some sex-specific developmental patterns emerged. Male immatures preferentially interacted with adult male groupmates, presumably to gain access to important social resources. Female immatures appeared to increasingly distance themselves from groupmates up to dispersal, but showed a sharp increase in sexual interest in coresident adult males immediately prior to dispersing. Although data on adolescents are limited, this phase in particular appears to be a time of critical importance to woolly monkey life histories in both males and females, and may be of particular interest for future research.

Keywords *Lagothrix* · Juvenile · Adolescent · Social behavior · Life history · Development

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C. A. Schmitt (✉)
Center for Neurobehavioral Genetics, Semel Institute for Neuroscience and Human Behavior, University of California, Los Angeles, CA, USA
e-mail: chris@evopropinquitous.net

A. D. Fiore
Department of Anthropology, University of Texas, Austin, TX, USA
e-mail: anthony.difiore@mail.utexas.edu

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8.1 Introduction

Primates are unusual among mammals in having the longest average period prior to reproductive adulthood relative to their body size (Schultz 1969; Read and Harvey 1989; Charnov and Berrigan 1993). Much debate and uncertainty surround the question of why such a long prereproductive phase should evolve given the high mortality risks associated with ages prior to adulthood observed in most primates (Janson and van Schaik 1993; Leigh 2001). This uncertainty has not been resolved, in part because juvenile and adolescent primates have only rarely been the focus of behavioral research (Pereira and Fairbanks 1993; Pereira and Leigh 2003), although there is a growing interest in the behavior, morphology, and development of immature primates as foci of research (Fellmann and Schmitt 2010).

The juvenile and adolescent phases are considered to be crucial times in the social development of immature individuals, as they are the periods when young primates prepare for and then learn how to navigate the social perils of the adult world (Pereira and Altmann 1985; Strier 1993). Atelin primates—which include the woolly monkeys (genus *Lagothrix*), muriquis (genus *Brachyteles*), and spider monkeys (genus *Ateles*)—have among the longest prereproductive phases of any primate clade outside of the hominoids (Blomquist et al. 2009; Di Fiore and Campbell 2007). Within the atelins, there is some sex-based and possibly phylogenetically informed variation in life history traits during development. In keeping with their relatively close phylogenetic relationship inferred by molecular methods (Wildman et al. 2009; Opazo et al. 2006), *Lagothrix* and *Brachyteles* females seem to share a life history pattern that emphasizes a more extended prereproductive phase for their body size compared to *Ateles*. While *Ateles* females begin to reproduce at around 7 years of age, current data on *Lagothrix* and *Brachyteles* suggest that they do not begin reproducing until around 9 years of age. By this metric, when controlling for adult female body mass, both *Lagothrix* and *Brachyteles* females mature almost twice as late as *Ateles* females (Di Fiore and Campbell 2007). Published ages at which male *Lagothrix* are estimated to begin copulating (3.5 years), however, suggest that they may mature much earlier than do either *Ateles* (4–5 years) or *Brachyteles* (5.5 years). In all three atelin taxa, males appear to reach sexual maturity—or to at least initiate adult sexual behaviors—several years earlier than females. Recent research on *Brachyteles*, however, suggests that the age at initiation of copulations—one of many markers that researchers use to gauge sexual maturity—may not accurately represent the actual age of sexual maturity or adult status, as male muriquis do not begin to sire young until over 2 years after their first observed copulations (Strier et al. 2011).

Although immature muriquis (e.g., Strier 1993; Martins and Strier 2004; Printes and Strier 1999) and spider monkeys (e.g., Vick 2008; Schmitt 2010; Rodrigues 2007) have been the foci of some research, typically in the context of long-term studies on adults, woolly monkeys have until recently seldom been the focus of extensive research at any age. The goal of this chapter is twofold. First, we hope to synthesize previous research done on immature atelins to provide a phylogenetic context for the life history patterns of woolly monkeys. Second, we will use this context to present new data from a study investigating the behavior and development of immature wild lowland woolly monkeys (*Lagothrix poeppigii;* sensu Groves 2001) from birth to dispersal at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador.

8.2 Defining Developmental Landmarks in Juvenile and Adolescent Woolly Monkeys

8.2.1 Weaning

In mammals, the juvenile phase is generally understood to begin at weaning, but weaning is best understood as a process rather than a single event (Lee 1996), and it can be difficult to pinpoint or describe in studies of wild primates. The difficulty in characterizing weaning itself has fostered the use of numerous behavioral landmarks as proxies for the end of the weaning period, such as the first intake of solid food, the onset of behavioral conflict between mothers and infants, resumption of maternal sexual activity, or the assertion of maternal control over access to the teat (Lee 1996; Lee et al. 1991). Bypassing direct references to weaning, Pereira and Altmann (1985) described the beginning of the juvenile phase as the point at which an individual can survive without the aid of its mother, although this definition is similarly difficult to operationalize.

Weaning data on more frequently studied atelins are sparse. In one long-term study of *Ateles belzebuth chamek* at Cocha Cashu, Peru, most immatures were weaned by 2 years of age, as determined through maternal rejection of nursing attempts (Symington 1987). In another long-term study of *Ateles geoffroyi* in the Otoch Ma’Ax Yetel Kooh Protected Area in Quintana Roo, Mexico, there was evidence of large individual variation in the time when weaning was complete, with ages ranging from 24 to 31 months (Vick 2008). The date range is similar for populations of *A. geoffroyi* at both Barro Colorado Island in Panama (Milton 1981; Campbell 2000) and Santa Rosa National Park, Costa Rica (cf. Di Fiore and Campbell 2007). In *Brachyteles,* weaning appears to occur between 18 and 24 months of age (Strier 1991), much earlier for their body size than in *Ateles*.

Outside of the new data presented in this chapter, weaning data are not available for wild *Lagothrix*. In captivity, infant woolly monkeys begin to eat solid foods from 45 to 71 days of age (Barnes and Cronin 2012), but there are no published data on nursing rates or weaning in either wild or captive populations.

8.2.2 Sexual Maturity

On the other end of the juvenile phase, sexual maturity can be equally difficult to define in wild primate populations. Perhaps, the most well-known cue of female sexual maturity is the anogenital and perineal (or sexual) swellings seen in catarrhines (e.g., Nunn 1999; Dixson 1983). Evidence of strong correlations between sexual swellings and the ovulatory cycle of both nulliparous and parous females suggests that swellings may be reliable indicators of the initiation of sexual maturity (Paoli et al. 2006). In platyrrhine primates, such as the atelins, however, sexual swellings have not been observed. Among lowland woolly monkey females, some changes in vulvar appearance—relatively swollen labia and a slight shimmer to the anogenital area—have been noted around the time when mating is common, but it is unclear if these are sexual swellings per se or a by-product of copulation (Schmitt, personal observation).

Most suggested indicators of ovulation in spider monkeys—such as urine sniffing, clitoral investigation, and aggression directed at females by males as well as clitoral self-manipulation in females—have been found to not correlate with female reproductive cycling (Campbell 2003, 2004; Campbell and Gibson 2008), and have not been systematically observed in woolly monkeys. In *Brachyteles,* it appears that the only observable indicator of the age at sexual maturity in females is the onset of male mating interest (Martins and Strier 2004). Anecdotal evidence from our study site suggests that such behavioral cues may be available in woolly monkeys, although it appears that it is the onset of *female* mating interest that might be an indicator. One radiocollared juvenile female ("Audrey"; group Y) showed marked behavioral changes immediately prior to dispersal, which included following, frequent approaching, and genital inspection of a big adult male (including sniffing, handling, and attempting to lick the scrotal tuft). One other unmarked subadult female ("Figment") in the same study group showed similar interest in adult males a few weeks prior to disappearing (Di Fiore et al. 2009). This approach–leave behavior and inspection are common in adult female sexual interest in both populations of *L. poeppigii* and *L. lugens* in Colombia, where females interested in copulation also bare their teeth and retract their lips in front of the male in a "teeth chatter" display (Eisenberg 1976; Nishimura 1988), accompanied by "clicking" noises (Murdock 1981; Nishimura 1988).

Female hormonal profiles and ovarian cycles have been used to monitor sexual maturity in atelins (*Brachyteles,* Strier and Ziegler 1997; *Ateles*, Campbell 2000), but they can be erratic at the onset of puberty (e.g., Strier and Ziegler 2000) and have not yet been assessed in woolly monkeys. Among females, the surest indicator of sexual maturity may be the first birth of an offspring, although studies in muriquis suggest that using this method may exclude up to almost a year in which a female may be cycling but not reproducing (Strier and Ziegler 2000).

For male primates, sexual maturity is often inferred through the development of secondary sexual characteristics. Adult males of many taxa demonstrate striking differences in body size, coloration, and various other features once full adulthood is reached (e.g., Plavcan 1999; Dixson 1997). In woolly monkeys, noted sexually dimorphic traits include marked differences in body size, musculature, and sex-specific patterns in hair growth and possibly glandular secretion patterns (Di Fiore and Schmitt, unpublished data). These traits, however, do not uniformly appear at puberty, and male secondary sexual characteristics may not fully develop until long after hormonal puberty begins. In mandrills, for example, males can successfully reproduce around 5.5 years of age when testicular mass increases dramatically, but secondary sexual characteristics generally develop much later: sternal scent glands and marked sexual coloration begin around 6–7 years, mass growth peaks at 7–8 years, and full adult male mass is not attained until 10 years of age (Setchell and Dixson 2002; Setchell 2003).

The loose relationship between sexual maturity and secondary sexual characteristics can also be confounded by social interference. The rate and extent of male secondary sexual characteristic development have been described as a function of social status and dominance in several primate taxa with marked dimorphism (e.g., mandrills: Setchell and Dixson 2001; orangutans: Maggioncalda et al. 1999; Utami and van Hoof 2004). Such cases of late-onset development of secondary sexual characteristics, or bimaturism, in reproductively capable individuals suggest that caution must be used when using such traits to interpret reproductive status. Whether such social interference occurs in woolly monkeys is as yet unknown. Dominance relationships in *L. poeppigii* have been difficult to characterize (e.g., Di Fiore and Fleischer 2005). Although males in *Lagothrix* are noted to be consistently dominant over females (Nishimura 1994; Di Fiore and Fleischer 2005), within-group male dominance relations appear to be tolerant and, if anything, based solely on body size. There is no evidence yet indicating that social interference from large adult males has an impact on juvenile or subadult male development.

8.2.3 Dispersal

Dispersal from the natal group is often understood to be a sign that sexual maturity has occurred, or is at least imminent, and is thought to be a mechanism to either avoid inbreeding or increase reproductive opportunities (Greenwood 1980; Moore and Ali 1984; Clutton-Brock 1989; Moore 1993). Traditionally understood proximate mechanisms for dispersal support the idea that sexual interests dominate dispersal decisions, either through the forced eviction of maturing individuals by resident potential competitors or through the attraction of possible sexual partners to dispersing individuals (Pusey and Packer 1987).

The proximate mechanisms underlying dispersal, however, may not in fact involve the reproductive status of dispersing individuals. In a study on *Cebus capucinus,* the strongest predictor of natal dispersal among juvenile males, regardless of age, was instability in social relationships among natal-group males (Jack and Fedigan 2004a). In the same study, dispersal decisions were also strongly influenced by parallel emigration, or the emigration decisions of coresident males and the presence of related and natal-group males in another group that a disperser joined (Jack and Fedigan 2004a). In muriquis (*Brachyteles hypoxanthus*), female dispersal almost always occurred prior to sexual maturity and appeared not to be instigated by aggression or reproductive suppression (Strier and Ziegler 2000; Printes and Strier 1999). The disappearance or dispersal of an individual, then, is not a reliable indicator of sexual maturity and should instead be understood as an important behavior that may or may not occur within the bounds of the juvenile phase.

Evidence of predispersal and dispersal behavior in *L. poeppigii,* specifically with data collected in this study and from previous studies with the same social groups at TBS, has been discussed extensively elsewhere (Di Fiore et al. 2009). Only a brief discussion will be outlined below. Dispersal in woolly monkeys has traditionally been characterized as female-biased (Di Fiore and Campbell 2007), although *Lagothrix* appears to deviate significantly from female-biased dispersal patterns. A summary of known or inferred dispersal events with detailed behavioral descriptions can be found in Di Fiore et al. (2009).

Dispersal in woolly monkeys has been difficult to characterize. Female-biased dispersal has been observed in the genus *Lagothrix* (Nishimura 1990a, b, 2003; Stevenson et al. 1994; Stevenson 2002), although more recent genetic data in *L. poeppigii* have indicated that both sexes may be dispersing (Di Fiore and Fleischer 2005; Di Fiore et al. 2009). Within the study groups at TBS, genetic data and behavioral observations suggest that both males and females may disperse in a variety of ways, both prior to and after reaching sexual maturity.

8.3 Social Structure and Sex-Specific Development

Although the data presented in this chapter are largely descriptive, the presumed social structure of woolly monkeys provides a theoretical framework under which we can predict certain patterns in development. The social relations of juvenile woollies should, for example, reflect the patterns of philopatry and dispersal seen in adults. As Walters (1987) noted, the social environment of the natal group is only of long-term importance to those individuals that plan on staying. Social investment in the group then—evidenced through affiliative social behaviors and association with groupmates—should differ by sex if there is sex-biased dispersal and philopatry. Association preferences in play and grooming for matrilineal kin and high-ranking females in female-bonded taxa, wherein maternal rank may influence the social success of immatures, are apparent in several cercopithecids (e.g., in *Papio:* Pereira 1988; *Erythrocebus:* Rowell and Chism 1986; *Chlorocebus:* Fairbanks 1993; Fairbanks and McGuire 1986; Raleigh et al. 1979; *Macaca:* Nakamichi 1989; Ehardt and Bernstein 1987; Glick et al. 1986; *Cercocebus:* Range 2006; *Presbytis:* Nikolei and Borries 1997). In more egalitarian cercopithecids, such as *Cercopithecus mitis,* juveniles appear to prefer maternal kin and direct same-sex associations to partners of high rank. In this case, it is presumed that males benefit from same-sex associations to build bonds of support that may benefit them during parallel dispersal (Cords et al. 2009). Among New World monkeys, a similar pattern can be seen in *Cebus,* wherein immature males appear to prefer male association partners that can also benefit them during parallel dispersal (e.g., Jack and Fedigan 2004a, b), and females seek out both matrilineal kin and high-ranking individuals that will benefit them most when negotiating their way into the adult social sphere (Perry 1996).

Atelin primates present a unique challenge to assessing social roles in that they appear to socialize only very rarely. In most studies of atelins, spatial relations can be used as a reliable indicator of association in lieu of actual social interactions (e.g., Stevenson 1998; Strier 1993). In a study of immature muriquis (*B. hypoxanthus*), in which female dispersal is the norm, Strier (1993) found that subadult males shifted spatial association preferences from adult females to adult males as they aged, presumably reflecting the importance of male associations to future social success as resident males in their natal group. Juvenile females, however, also preferentially associated with adult males, the benefits of which were unclear given the expectation of dispersal (Strier 1993).

In woolly monkeys, adult males are generally tolerant of each other and will cooperate during aggressive intergroup encounters (Nishimura 1990a; Di Fiore and Fleischer 2005). Males are occasionally seen roving in all-male groups (Di Fiore 1997; Di Fiore and Fleischer 2005; Di Fiore et al. 2009), although affiliative behaviors between adult males are rarely observed (Nishimura 1990a; Di Fiore 1997; Di Fiore and Fleischer 2005). Adult male association is rarer in *Lagothrix* than in other atelins, but the circumstances under which it occurs—such as mate and territorial defense—suggest that the establishment of male bonds may be important. Woolly monkeys have been characterized to have male philopatry and female-biased dispersal, but recent genetic and behavioral evidence suggests that this pattern may not be strictly followed (Di Fiore et al. 2009).

Despite the apparent flexibility of patterns of dispersal and philopatry in males, mature females do not typically remain in their natal groups to mate (Nishimura 2003; Di Fiore and Fleischer 2005), and females appear to be even less social with other females than in other atelin taxa (Di Fiore and Campbell 2007). Previously noted patterns of affiliation indicate that the most frequent affiliative partners are adult and subadult males, and adult males and females (Di Fiore 1997; Di Fiore and Fleischer 2005; Stevenson 1998). Given the social patterns seen in adults, immature male woolly monkeys can be expected to seek out associations with adult males, while immature females can be expected to remain relatively solitary outside of the mother–offspring relationship until dispersal (Sakurai and Nishimura 2000; Stevenson 1998). A possible exception to this expectation would be immature female affiliations with other females that might aid with parallel dispersal (either other immature females or mature females from neighboring groups during times of multigroup cohesion); however, the general absence of affiliation among adult females, or association generally, seems to preclude this possibility.

8.4 Methods

8.4.1 Study Area

Research was conducted at the TBS, located in the Yasuní Biosphere Reserve in lowland Amazonian Ecuador. Di Fiore and colleagues have studied woolly monkeys in the Yasuní region for varying periods of time since 1994 (Di Fiore 1997, 2003, 2004; Di Fiore and Fleischer 2005; Di Fiore et al. 2006; Di Fiore and Suarez 2007; Di Fiore et al. 2009). Behavioral data collection on woolly monkeys at TBS began in 2005 (e.g., Schmitt et al. 2007; Di Fiore et al. 2009).

The TBS site covers a series of rolling hills and drainages on the north side of the Río Tiputini (76°08′W, 0°38′S) and consists largely of undisturbed moist tropical rainforest that receives an annual rainfall of over 3,200 mm (Di Fiore and Rodman 2001). Within the site, an extensive network of more than 40 km of well-maintained, mapped trails covers an area of 600+ ha of terra firme and seasonally flooded forest. The home ranges of multiple social groups of each study species have been characterized and are contained, at least partially, within the established trail system.

8.4.2 Study Population

The subjects for this study include three habituated groups of woolly monkeys (*L. poeppigii*) that ranged within the trail system of TBS. Composition of each group was known, and births and disappearances were recorded when noted (Table 8.1).

Group Y was the largest (with around 30 individuals) and most well known of the three woolly monkey groups. Research and habituation with this group began in the summer of 2006. The home range of group Y encompassed the biological station and several home ranges of previously studied monkey troops from other projects, making data collection relatively easy compared to the other two groups. Group Y had a highly skewed sex ratio among immatures, with many more females than immature males. The group has been radiocollared since the summer of 2007, and several individuals in the group were also outfitted with identification collars (see below), allowing for easier identification of the group.

Group D was also fairly well known, with work on this group having begun sporadically in 2006 and increased in 2008 with the radiocollaring of an adult male group member. Group size was slightly smaller than in group Y, with roughly 25 individuals; the smaller group size is mainly attributable to a reduced number of adult females and associated offspring. The sex ratio among immatures in this group was highly biased towards males.

Group I was the least habituated and most difficult to follow of the three woolly monkey groups and was also the farthest from the biological station. An individual in group I was not radiocollared until March 2008, after data collection for this

Table 8.1 Consensus group compositions for TBS *L. poeppigii* study groups 2008–2009

Age/cohort	Social Group		
	Group D	Group I	Group Y
BAM	3.5	3.5	3
SAM	1	1	1.5
AF	8	8	10
2005+ (SUB)	3	5	5
M	3	3	1
F	0	2	3
2005 (JUV2/SUB)	2	2	3
M	1	1	1
F	1	1	2
2006 (JUV1/JUV2)	2	1	4
M	2	0	1
F	0	1	3
2007 (JUV1)	4	0	4
M	2	0	0
F	2	0	4
2008 (INF1/INF2)	2	3	4
M	1	1	2
F	1	2	2
2009 (INF1)	3	2	2
Total	*22.5*	*23.5*	*30.5*

Partial values reflect a change in numbers during the study period (either by age class graduation or by disappearance). Age classes assigned to individuals during the course of the study are listed next to each age cohort. Consensus group sizes are probably smaller than actual group size because of difficulty in identifying individuals and large group spread. Sex could not be determined for the 2009 cohort prior to the end of the study

project had already begun, leaving this group relatively undersampled compared to groups D and Y. The sex ratio of immatures in group I was relatively small. Group I was also the smallest of the three woolly monkey groups, with roughly 23 individuals.

The territories of groups D and Y overlapped extensively (see Di Fiore and Schmitt, this volume), with relations between the two groups varying from complete tolerance and coranging (where both groups mixed and ranged together for up to several days) to overt aggression and fighting (Schmitt and Di Fiore, unpublished data). Group Y territory also overlapped with those of at least three other woolly monkey groups, with similarly variable intergroup relations. The territories of groups D and I also overlapped, though not as extensively as in groups D and Y. Compared to groups D and Y, intergroup encounters between group D and group I were rare. The high territorial overlap between all study groups was extensive, suggesting that the variation in ecological conditions faced by the groups may not be high. Although the three *Lagothrix* groups live in consistent and primarily separate territories, and have very different sex ratios in juveniles, preliminary tests looking for variation in behavioral measures across groups showed few significant differences, and thus, analyses pooled data from all three *Lagothrix* groups together.

Throughout the study, monthly developmental assessments were made of identifiable immature individuals, and known individuals were "graduated" into the next age class based on observer consensus at the beginning of the appropriate month. Group composition changed accordingly by month, although a consensus group composition constructed from the total study period was used in those analyses that required such information.

Individual subjects were assigned to one of the following age/sex categories: adult male (AM), adult female (AF), subadult male (SM), subadult female (SF), juvenile male 2 (JM2), juvenile female 2 (JF2), juvenile male 1 (JM1), juvenile female 1 (JF1), infant 2 (INF2), and infant 1 (INF1). For some analyses, adult males were subdivided into big adult males (BAM) and small adult males (SAM) based on how strongly secondary sex characteristics were expressed. For analyses in which age class alone was used (rather than both age and sex class), these classes included adult, subadult (SUB), juvenile 2 (JUV2), juvenile 1 (JUV1), infant 2 (INF2), and infant 1 (INF1). Age/sex categories were assigned by a combination of characters including body size and proportions, development of secondary sexual characteristics and genital traits, and pelage appearance specific to *Lagothrix* (Table 8.2). Although behavioral landmarks (e.g., infant excursions from the mother, weaning processes) are used in some studies to define age/sex classes (e.g., Nishimura 1990a for *L. lugens*), they were not used as primary indicators here as this study sought to compare variation in behavioral development among and between age/sex classes.

In order to locate groups and individually identify difficult-to-distinguish woolly monkeys, at least one animal from each study group was anesthetized via remote injection, captured, and outfitted with a very high frequency (VHF)-transmitting radiocollar (Holohil^{TM}) for use with telemetry. To aid in individual identification,approximately six additional animals in each study group were darted and outfitted with ID collars, consisting of a fitted stainless steel ball-chain collar with two affixed aluminum tags of varying color and shape combinations, similar to those used in other long-term studies of nonhuman primates. The remote anesthetization protocol used for this project was developed with the assistance of the New York University veterinary staff and was approved by the Institutional Animal Care and Use Committee (IACUC) at New York University.

8.4.3 Data Collection

Data for this study were collected from January 2008 to November 2009, by eight different observers (see below for a discussion on interobserver error). All data collectors were scheduled to follow study groups for 3–4 days consecutively from sunrise to sunset before switching to a new group, and groups were rotated regularly through each month for the duration of the 23-month study to ensure that equal time was spent with each group. The final amount of behavioral data is roughly equivalent, with slightly more data collected for the most habituated study

Table 8.2 Identifying features of age/sex classes in *L. poeppigii* based on physical features

Temporal age	Age class	Sex	Physical features
0–5.5 months	Infant 1 (INF1)	M/F	Thin and wispy yellow fur, through which black skin can be seen; vulva depigmented and visible from birth, continues through adulthood, with the labia majora darkening to varying extent during development
5.5–12 months	Infant 2 (INF2)	M/F	Fur darkens to silvery-brown, may appear orange; fur thickens, becomes fluffier, skin no longer visible through fur
12–23 months	Juvenile 1 (JUV1)	M/F	Fur still silvery-brown and fluffy, bodily proportions appear compact compared to older juveniles and adults (e.g., short limbs relative to body size). In males, genitalia are black, sometimes with depigmented areas; penis and scrotum are small, testes not discernible
23–?? months	Juvenile 2 (JUV2)	M/F	Fur loses silvery tone and becomes less fluffy-looking, more adult-like in texture; testes are more visible in males, although not enlarged, and outline of both can be seen in the scrotum. Bodily proportions appear gangly, and individuals often appear thin
33–?? months	Subadult (SUB)	M	Body size is much smaller than that of adult males, but testes are fully descended. Development of secondary sexual characteristics aside from testis size is lacking
		F	Body size slightly smaller than adult females, still somewhat gangly in body proportions and do not have the "bulk" of fully adult females
?? months	Adult	M	*Small adult male (SAM)*: Body size and musculature bulks up a bit, some development of secondary sexual characteristics; ring of hair around scrotum fills out and hair along midline of chest darkens and lengthens; penis lengthens (this phase may be more correctly assigned to subadult status) *Big adult male (BAM)*: Marked development of secondary sexual characteristics; scrotal tuft is large and conspicuous as are testes and scrotum; temporal and masseter muscles become very conspicuous; hair along midline of the chest is very long, dark, and may appear slick due to waxy secretions from sternal gland; shaft of penis becomes thicker
		F	Some adult females "bulk up" in body size, but temporal and masseter muscles do not become more developed as seen in BAM. Some have visibly elongated nipples (presumably multiparous). When much older, fur especially on midline of chest, gets longer and darker while the hair on the pectorals thins. Clitoris and caudal end of the vulva remain depigmented, while the cranial labia may darken to a variable extent. Vulva seems more naked and may appear more "full" compared to subadults, and may appear swollen during certain phases of the reproductive cycle

Temporal age limits are averages of observed individuals' age/class graduation dates

Table 8.3 Contact hours and number of focal and scan samples collected in the this study

	Group D	Group I	Group Y
Contact hours	739.8	551.5	926.3
Focal samples	352	310	444
Scan samples	769	717	1,195

group (group Y; Table 8.3). Study groups were found using telemetry on a radiocollared individual in each group. Data collection within the day was divided by 3-h intervals in which observers attempted to collect three focal animal samples (FAS) and three scan samples.

8.4.4 Developmental Measures

In order to establish more accurate assessments of age/sex class, as well as to establish meaningful correlations between developmental phase and behavior, all immature individuals were assessed once each month by each observer. Assessment included filling out a work sheet on developmental landmarks attained. The majority of the landmarks were qualitative descriptions of physiological indicators of maturity and development, such as pelage color and quality; relative size, color, and development of genitalia; development of secondary sexual characteristics (such as musculature and scrotal tufts); and size relative to adult individuals. Behavioral landmarks of development (e.g., weaning process, locomotor independence, dietary development, primary social partners) were also summarized monthly by consensus among all observers present at the field site collecting data for this study, and included in the work sheet to guide comparisons between physiological and behavioral development.

8.4.5 Behavioral Sampling Methods

Focal Animal Samples

Behavioral data of 369 hours were collected during 2,217.6 contact hours using 20-min FAS (Altmann 1974). Instantaneous observations within a single focal sample are not statistically independent. Therefore, I treated each FAS as a data point for subsequent analysis. Point samples (PS) were taken at 2-min intervals within each FAS, wherein the behavioral state of the focal animal and the identity, age/sex class, behavior, and proximity of its “nearest neighbor” (NN) were recorded. The NN of an animal can provide valuable information on the social preferences of each animal, even when behavioral information may be lacking. Additionally, every 4 min, an instantaneous scan was taken within the context of the FAS representing the behavior and social context of the focal animal. Each instantaneous scan consisting of the identity, age/sex class, behavior, and proximity of two NNs (typically the primary caregiver and a second NN), and the identities or age/sex classes of all individuals in close proximity (within 1 m) and within 10 m were also taken so that the social context of the focal animal could be tracked within focal samples and correlated with the continuous behavioral data.

The target for all data collectors was to collect one complete FAS every hour during the day. Because woolly monkeys are often high in the canopy and spatially dispersed (e.g., Stevenson and Quiñones 1993; Stevenson et al. 1998), some group members are often out of view from the ground, making it difficult to follow a schedule of rotation among focal subjects. Thus, animals were chosen for FAS opportunistically, based on visibility when a sample was started, with the following restrictions: (1) FAS of the same individual had to be separated by at least 20 min and (2) if many individuals were visible, then the one sampled least recently should be chosen. An attempt was made to cover all individuals present, and data collectors kept a tally of FAS collected to balance sampling across individuals, age/sex classes, and time of day. Behavioral data were collected using an ethogram modified from Di Fiore (1997; 2003).

Scan Samples

A total of 1,273 instantaneous scan samples (Altmann 1974), representing 3,530 individual scans, were taken opportunistically throughout the day when FAS were not possible, with a target of one scan every hour of all animals in immediate view. Due to the diffuse spatial cohesion of *Lagothrix,* the number of individuals represented in scans varied considerably (range = 1–10, mean = 2.7, standard deviation (SD) = 1.1). Scans included data on behavioral state, position in the group, group or subgroup size, and composition for each animal in view. Individual identity, age/sex class, behavior, and distance to the NN were also recorded, as well as the identity of age/sex class, as best possible, for all individuals in close proximity (within 1 m) and within 10 m for all scanned individuals. It should be noted that scan samples have been observed to overestimate conspicuous behaviors, such as moving and socializing (e.g., Altmann 1974; Stevenson and Quiñones 2004).

Nursing Bouts

If nursing was observed during other data collection routines, the collection of the nursing data received priority. Information collected on nursing followed the guidelines suggested by Lee (1996, 1999). Data collected ad libitum during a nursing bout included the identity and age/sex class of the nursing individual, identity of lactating female, and detailed behavioral data including initiation and termination time and the identity of the terminating individual.

Interobserver Reliability

Eight people collected data over the course of the project, and CAS overlapped with and trained all but one, who was trained by assistants with 6 months of prior experience with the project. Training of assistants consisted of guided observations in the field and the studying of an extensive protocol outlining the data collection regime. Observer data were not used until the observer had been trained for 3 weeks, when deviations from experienced observer data were demonstrably low. Interobserver reliability was assessed at the beginning of each month and during the first 3 weeks of an assistants' time on the project, when all present assistants went to the field concurrently and collected data within the same group. Data that showed consistently high interobserver error were excluded from data analysis. Post hoc assessments of interobserver reliability using statistical comparisons of behavioral variables across observers (such as activity budgets and frequencies of specific behaviors) in same-age/sex classes show most interobserver differences to be statistically insignificant. In those cases where interobserver differences were statistically significant, the data of the most inconsistent observer were excluded from that analysis, and the data were retested again across the remaining observers.

On Individual Identification

Although individual identification is of great importance to studies on social behavior—not only to decrease the probability of type 1 errors and to draw out patterns that may be individually specific but also to assess the role of kinship or interindividual bonds on social behavior (Leger and Didrichsons 1994; Altmann 1974)—it was often not possible to identify individual woolly monkeys in this study. Repeated attempts at marking individuals noninvasively—such as with paintballs with nontoxic paint and dye darts filled with commercial hair bleach—were fruitless, presumably due to the relatively oily fur of woolly monkeys and the frequent heavy rains at the study site. We had far greater success placing ball-chain identification collars on individuals, but our reluctance to anesthetize juveniles and our choice to avoid darting mothers with dependent offspring—to avoid injuring those offspring from a subsequent fall from the canopy, inadvertently darting the offspring, or leaving a young individual without contact with its mother for several hours—prevented us from collaring more study subjects. Although we outfitted several adult females with identification collars in the groups followed for this study, many of the collared females either did not have offspring or no longer associated closely with them. Additionally, when the offspring of identifiable females left the proximity of their mother, they could no longer be identified with confidence. Care was taken to avoid oversampling the same individuals in the group (Ha and Ha 2003). Due to the lack of individual recognition, we pooled behavioral samples by age/sex class without regard to individual identification (Leger and Didrichsons 1994).

On Focal and Group Visibility

Given the density of the rainforest canopy, not all animals can be seen at all times, despite the best efforts of the observers. Invisibility issues were dealt within the field by entering the code “Fuera de Vista” (“FV”) whenever an animal was out of view. If there was a possibility that other animals could be out of view in a given proximity from a focal subject during a PS or scan (e.g., if the focal subject was surrounded by dense foliage or near a thick vine tangle), the code “FV” was placed in the given proximity level. For the sake of simplicity, samples with “FV” entered for a proximity value were excluded from analyses in which proximity was a variable.

Although every effort was made to see all animals in a certain proximity to data subjects, this may not always have been effective. It is possible that the missing data of invisible animals could change the outcome of statistical tests. To measure this possible effect in all tests that relied on proximity data, I ran post hoc proximity-based tests with 1 % invisibility, 5 % invisibility, and 10 % invisibility of animals in proximity. It is unlikely that observers consistently missed seeing individuals in proximity more than 10 % of the time. For each percentage of presumed invisibility, I randomly added one animal to the proximity values in the presumed percentage of data samples. This was only done at the proximity level within 10 m, as observers never had visibility problems within 1 m of a data subject that would not have been assigned an “FV” value and discarded. The same statistical tests were then rerun with the added “invisible” animals. Although the addition of animals in the 10-m proximity range did change the p values slightly, the significance of the results never changed, suggesting that the results of proximity tests presented subsequently are robust even given an “invisibility factor” of up to 10 %.

8.4.6 Data Analysis

Nonparametric statistical tests were used to accommodate small sample sizes and stubbornly nonnormal datasets. All statistical tests, unless otherwise noted, were run using the statistical programming package R (R Development Core Team 2012).

Instantaneous observations within a single focal sample are not statistically independent. Therefore, I treated each FAS as a data point for analysis. Numerical variables, such as the number of individuals in a given proximity and distance to NN, were all averaged within each FAS (e.g., Di Fiore 2003) and were then pooled within age/sex classes (Leger and Didrichsons 1994). The process of using pooled data within age/sex classes, necessitated by the limited individual recognition possible for woolly monkeys, allows for pseudo-replication in the dataset, which may cause the behavioral patterns of overrepresented individuals to drive trends that are then attributed to the entire age/sex class. Additionally, in pooling data from all individuals within a given age/sex class together, we can no longer appreciate or investigate the variety of individual strategies that may be at work. Finally, without individual recognition, kinship, and specific interindividual relationships cannot be taken into account.

Table 8.4 Consensus table of age grade timing in months from birth in *L. poeppigii*

Sex	*N*	INF2 begin	*N*	JUV1 begin	*N*	JUV2 begin	*N*	SUB begin	*N*	SUB end…
Male	3	4 mo	1	< 19 mo	3	20–25 mo	4	29–36 mo	1	60+ mo
Female	4	4–7 mo	6	9–14 mo	1	26 mo	0	–	1	36+ mo

Where multiple age/sex classes were compared for values of proximity or NN distance, a Kruskal–Wallis test was performed to assess whether the median value differed across age/sex classes. If results were significant, a Nemenyi–Damico–Wolfe–Dunn test (a nonparametric version of Tukey's honest significant difference, HSD) was used to assess which pairwise comparison was driving the significant results. The alpha level was set at 0.05 for all tests except the Nemenyi–Damico–Wolfe–Dunn test, in which the alpha level is set to 0.01 to correct for multiple pairwise comparisons. Results are reported as the mean value ± standard error. In cases where proportions of associations by age/sex class are reported relative to group composition, a chi-squared proportion test was used. Hinde indices are reported using a modified version of the index (Brown 2001).

8.5 Results

A total of 30 identifiable immature woolly monkeys were followed throughout the study period, during which time dates of "graduation" were recorded for 17 individuals when physical characteristics matched those determined for the succeeding age/sex class (Table 8.4). Not all individuals contribute to the dataset every month due to either absence of data collection or simply not having seen certain individuals; therefore, some graduation dates between age classes are approximate or missing. From those individuals observed across multiple age classes, we were able to construct a consensus table of date ranges during which graduations from one age class to the next occurred within the study groups (Table 8.4). There were too few identifiable individuals within each age/sex class, however, to reliably compare developmental timing between sexes.

The longest phase prior to reproduction appears to be subadulthood (Fig. 8.1). In *Lagothrix,* each infant phase lasted about 6 months, and there was a roughly yearly progression from one age grade to another once the juvenile phases were reached. Upon reaching subadulthood, however, there was very little resolution in age grades among females. The four females that are suspected to have undergone dispersal ("Audrey," "Figment," "Sasha," and "Roosevelt"; see below) could not be appropriately aged in the context of this study. The one subadult female that is suspected to have emigrated into her study group ("Roosevelt") still appeared to be a young subadult at the time of her immigration. Among males, subadulthood appeared to last for at least a few years. One male that was noted to be a subadult in group Y in the summer of 2006 ("Hemlock"; his scrotal tuft was just beginning to grow a

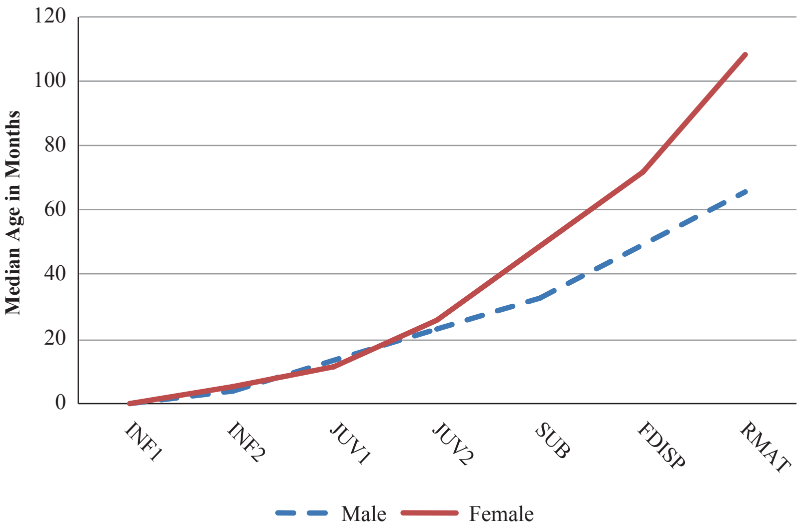

Fig. 8.1 Timing of age grades and landmarks in immature and adolescent woolly monkeys. *FDISP* indicates female dispersal age, and is taken from Di Fiore and Campbell (2007) while *RMAT* indicates age at reproductive maturity

corona of fur) was still identified as a subadult in the group in October 2008—the fur of his scrotal tuft had still not filled out completely and he had not yet developed the full suite of secondary sexual characteristics denoting a SAM—suggesting that a significant amount of growth must still be attained once males have presumably begun sexual maturity.

8.5.1 Proximity: Age Differences

Woolly monkeys showed significant differences in the number of individuals in close proximity (within 1 m) based on age class (Kruskal–Wallis $X^2=191.93$, df=5, $p<0.001$), apparently due to the close relationship between young immatures and their mothers. A post hoc test of pairwise differences between age classes suggested that the number of neighbors in close proximity remains similar throughout juvenescence before dropping off significantly upon reaching subadulthood (Fig. 8.2a).

The number of individuals in proximity within 10 m was also significantly different across age classes (Kruskal–Wallis $X^2=37.11$, df=5, $p<0.001$), but the only significant pairwise differences observed in proximity patterns within 10 meters were between young infants and both adults and subadults (Fig. 8.2b). Mother–offspring bonds with previous young that were not yet subadult may have influenced these more distant proximity patterns for INF1 individuals, as the prior offspring of mothers with newborns often remained in loose association with their mothers.

Hinde proximity index scores between age/sex classes suggested that effort for maintaining close proximity to adults shifts to immature individuals as they age

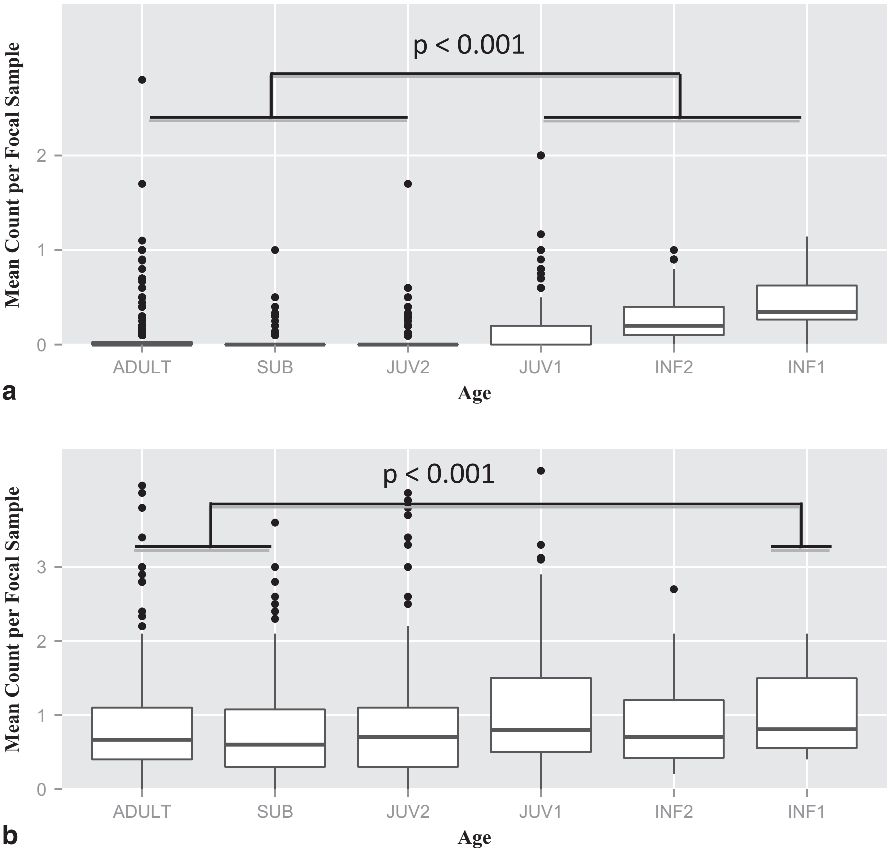

Fig. 8.2 Mean number of individuals in proximity within **a** 1 m and **b** 10 m by age class

(Table 8.5). Close proximity maintenance was roughly even between adult females and immatures (aside from the relatively immobile INF1 class). BAMs were responsible for maintaining close proximity to all younger immatures (JUV1, INF2, INF1), but there was an even effort in maintaining close proximity to BAMs among all other older age classes. There were no clear patterns in proximity maintenance among immature age classes, and subadults did not appear to seek out close proximity with other groupmates except for adults.

8.5.2 Proximity: Sex Differences

Overall, immature males spent significantly more time with other males in close proximity compared to immature females (immature males, $n=324$, mean=0.049; immature females, $n=299$, mean=0.025; $W=31{,}743$, $p<0.05$), although the mean

Table 8.5 Hinde proximity index scores between age/sex classes

Actor		Recipient									
		Adult		SUB		JUV2		JUV1		INF2	INF1
		M	F	M	F	M	F	M	F		
Adult	M		43	50	50	43	25	75	74	75	100
	F			11	50	71	60	62	52	58	67
SUB	M				71	35	50	39	60	–	–
	F					50	–	25	25	–	100
JUV2	M						60	62	100	75	100
	F							100	56	100	100
JUV1	M								83	0	100
	F									33	–
INF2											–
INF1											

Using the Brown (2001)-modified Hinde proximity index score, a score above 50 indicates that the actor is primarily responsible for maintaining proximity. Dyads for which no change in proximity was recorded are listed as "–"

number of males per FAS was so low as to be of questionable import; no significant difference was found within 10 m ($W=29{,}273$, $p=0.587$). Sex-specific preferences for spatial associations—aside from a significant increase in proximity to adult females in immatures compared to adults, apparently driven by mother–offspring bonds (Kruskal–Wallis $X^2=40.05$, df=10, $p<0.001$)—were not found. Within males overall, a spatial preference for close proximity to males of all ages, or to only adult males, was not found, although the limited sample of SAMs had significantly more adult males, and males in general, within 10 m than any other age/sex class. There was, however, a significant difference in preference for proximity to adult females between adult females (which appear to avoid proximity with other adult females) and juveniles and infants of both sex classes (which were often in proximity with adult females, presumably their mothers).

8.5.3 Proximity: Nearest Neighbors

To investigate NN patterns, the dataset was divided into separate sections for each group to accommodate differences in group composition. It was universal across groups that the NN of juveniles and infants was most often an adult female. In keeping with the proximity data, this proportion appeared to diminish within each sex as age class increased. Immature females kept adult females as their most frequent NNs up through the subadult phase, often increasing the proportion of time spent with adult female NNs as subadults. Among immature males, the decrease in the proportion of PS with adult females as NN was accompanied by a concomitant increase in the proportion with adult males as NNs.

Table 8.6 Nursing bouts in *L. poeppigii*

	JM2	JF2	JM1	JF1	INF2	INF1
N	3	4	13	23	10	19
Mean bout length	1:11	1:11	1:06	0:50	0:33	1:27
Bout range	< 1–2:00	< 1–2:00	< 1–5:53	< 1–3:03	< 1–2:00	< 1–10:00
Ended by infant	1	4	10	13	4	6
Ended by mother	1	0	3	2	2	5
Proportion of FAS with nursing	1.9 %	3.2 %	10.8 %	14.5 %	16.7 %	31.3 %

There were some notable group-specific trends, although it is unclear whether and how group composition might mediate these trends. Group D, for example, had a higher proportion of immature males than the other two study groups, and while it was the impression of researchers that immature males self-segregated into an all-male cohort through most of the day, there was only mixed support for this in the data. There was no evident difference in proportions of immature males and females as NNs in either sex in the older immature age classes, but Juvenile 1 classes did appear to spend more time with same-sexed immatures as NNs. In group I, where the sex ratio among immatures was roughly equal, subadults of both sexes spent an equally large proportion of time with BAMs as the NN, which was roughly equal to proportions seen in their adult groupmates. Although group Y had a relatively high proportion of immature females compared to other study groups, this did not appear to drive trends in association.

8.5.4 Nursing

Nursing bouts were observed 72 times during this study and occurred from the infant 1 to as late as the juvenile 2 phase. As we did not conduct all-day follows of infants, we cannot estimate the frequency of nursing bouts throughout the day. There does not appear to be a pattern in mother versus infant termination of nursing bouts, despite expectations that mothers of older offspring would terminate nursing bouts more frequently due to parent–offspring conflict (Trivers 1974; Lee 1996). Nursing rejection, where mothers aggressively push away juveniles attempting to nurse, was observed only once and was directed against a JF2. Nursing bouts were generally less than a minute long, regardless of the age/sex class of the nursing individual, although nursing bouts in excess of 10 min were observed (Table 8.6).

Half of the nursing bouts observed were collected in FAS and the rest were collected ad libitum. All FAS were pooled together by age class, and the proportion of FAS for a given age class that contained a nursing bout was calculated and compared. As a proportion of all FAS, nursing was observed more frequently in infant classes, although the difference was not significant.

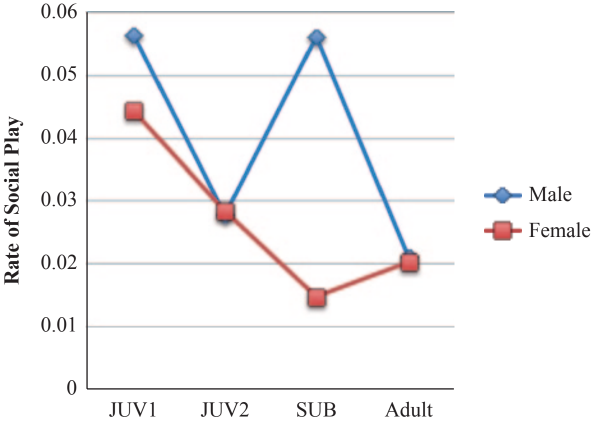

Fig. 8.3 Proportion of time spent in social play. Values were obtained by dividing the number of point samples that involved play by the total number of point samples collected within each age/sex class

8.5.5 *Social Play*

Consistent with previous reports in *L. lugens* (Nishimura 1990a), play in woolly monkeys consisted primarily of chasing and grappling in groups of 2–5 individuals. Overall, play bouts were most frequently observed among immatures ($n=44$), followed by bouts between adult females and their associated infants ($n=12$), and finally between BAMs with immatures ($n=6$). Play between immatures and BAMs most often occurred with immature males (BAM with JM, $n=5$; BAM with JF, $n=1$). The only play bout observed between adults was between two adult females.

The frequency of play bouts differed significantly by age class when controlling for sampling effort (Kruskal–Wallis $\chi^2=33.6468$, df=5, $p<0.001$). Play is often considered to occur significantly more often in immatures. In this study, the only significant differences in rates of play between age classes when controlling for sampling effort were found between the youngest immature age classes and adults (Fig. 8.3). Given female-biased dispersal, immature males would be expected to play more frequently than immature females, as males would benefit from establishing bonds with other male groupmates. Overall differences in the frequency of play behavior between comparably aged juvenile males and females, however, were not observed (JM2 vs. JF2, $p=0.897$; JM1 vs. JF1, $p=1$). With the exception of adult females and infant age classes (AF vs. INF2, $p<0.01$; AF vs. INF1, $p<0.01$), there were no significant pairwise differences between age classes within each sex in the frequency of play behavior.

8.5.6 *Grooming*

Grooming is generally rare in woolly monkeys, with only 103 bouts seen during the entire study period (71 observed during FAS, and 32 in scan samples; Table 8.7). As in previous reports of *L. lugens* (Nishimura 1990a) and *L. poeppigii* at a nearby site (Di Fiore and Fleischer 2005), adult males were groomed more than expected

Table 8.7 Percentage distribution of 103 grooming bouts observed in focal and scan samples by age/sex class of the groomer and recipient

	BAM	SAM	AF	SM	SF	JM2	JF2	JM1	JF1	INF2	INF1	Total
BAM	–	–	5.8	–	1.0	1.0	–	–	1.0	1.0	–	9.7
SAM	1.0	–	1.0	–	–	–	–	–	–	–	–	1.9
AF	6.8	2.9	9.7	–	2.9	1.0	6.8	1.0	1.0	2.9	4.9	39.8
SM	4.9	–	1.0	–	–	–	1.0	1.0	1.0	1.0	–	9.7
SF	1.9	–	2.9	1.0	1.0	–	–	–	–	–	–	6.8
JM2	3.9	–	3.9	–	–	–	–	1.0	–	–	–	9.7
JF2	1.0	1.0	2.9	–	–	1.0	2.9	–	1.0	–	–	9.7
JM1	–	–	1.0	1.0	–	1.0	1.0	–	–	–	–	3.9
JF1	1.0	–	4.9	–	–	–	–	–	1.0	–	–	6.8
INF2	–	–	–	–	–	–	–	–	–	1.0	–	1.0
INF1	–	–	1.0	–	–	–	–	–	–	–	–	1.0
Total	20.4	3.9	34.0	1.9	4.9	3.9	11.7	2.9	4.9	5.8	5.8	100.0

by chance, given their proportional representation in the population (chi-squared test: $\chi^2 = 17.7$, df = 10, $p < 0.06$). JF2s also received more grooming than would be expected by chance given group compositions, while subadults of both sexes and JM1 received much less. Immature males were not often observed to receive grooming, and they consistently received both proportionately and absolutely less grooming than expected by chance compared to same-aged females (chi-squared test: $\chi^2 = 5.01$, df = 1, $p < 0.05$). This sexual difference in the receipt of grooming effort is reversed upon reaching adulthood. As in previous studies, BAMs and adult females were most often the recipients of grooming, but unlike previous studies there was no significant difference in the receipt of grooming by sex in adults, although males did receive proportionately more than females.

8.5.7 Social Interaction Between Adult Males and Immatures

Adult male woolly monkeys appear to express great interest in infants. At least six instances of intense male interest were observed, in which males inspected, touched, and vocalized infants aged from just after birth to up to 3 months of age. Adult females controlled these interactions both by tolerating the behavior and by even appearing to solicit it by approaching BAMs and presenting their infants to them by laying down near them on a branch ($n = 3$). During these interactions, the BAM often placed his face directly against the infant's body, and his throat could be seen vibrating as his lips moved, suggesting a low vocalization (perhaps similar to "teeth chattering," although it seems similar to the "gecker" or "staccato" vocalizations described in a similar context in *C. capucinus;* Gros-Louis et al. 2008). Females were often responsible for ending the interactions ($n = 4$), typically by encouraging dorsal mounting by the infant and then leaving the male. In one instance, the male followed the female afterwards for several minutes. The sex of the infant involved could only be discerned in two cases, one male and one female, so there is no strong evidence for a sex bias in attention.

Intense interest in noninfant immatures was rarely seen outside of play contexts, although some exceptions were observed. In two separate cases in different groups, a BAM and a JM2 were observed participating in long (over 10 min; very long for a woolly monkey) mutual grooming bouts. These bouts were characterized by erections in both adult and juvenile participants (although no sexual contact resulted), and by slow and deliberate movement on the part of the juvenile male, who provided the majority of the grooming. In both cases, the juvenile male focused on grooming the scrotal area of the adult, often inspecting and licking the scrotal tuft. These interactions would end with one or both individuals abruptly leaving.

8.5.8 Sexual Behavior in Immatures

Sexual behavior in immatures was primarily seen in older age classes. Among males, erections could be seen in individuals JM2 and older, typically in the context of an interaction with an adult male (see above). Males whose secondary sexual characteristics were less developed than a BAM were never observed copulating with females. In group Y, a young AF was observed actively soliciting a SAM by grimacing at him while grooming him. Although the SAM had an erection, he was also consistently watching a large BAM within view 15 m away. After about 5 min of no response from the SAM, the AF left. Masturbation by manual stimulation was observed only once, in a young BAM; the bout had begun prior to the observer's arrival and lasted 5 more minutes before the male stopped, without evidence of having ejaculated.

Among immature females, sexual behavior was only observed in two subadults immediately prior to their presumed dispersal. In group D, an SF ("Sasha") was noticed following a BAM ("Dante") very closely. Sasha approached Dante while he rested in a crook in a tree, and inspected his scrotal tuft. During the inspection, she grimaced and licked the tuft repeatedly. After less than 2 min, Dante got up and walked away, followed by Sasha. Shortly after that interaction, Sasha disappeared from the group and is presumed to have dispersed. A similar set of behaviors was noticed in an SF ("Audrey") directed towards a BAM in group Y in the last 2 weeks she was observed ranging with that group (Di Fiore et al. 2009). These results are consistent with previous observations in *L. lugens* in Colombia, in which subadult females were rarely observed engaging in sexual activity before emigration from the natal group (Nishimura 2003).

8.5.9 Immature Involvement in Adult Copulations

Although immatures may not be involved directly in copulations, immatures are often caught up in the copulatory behavior of adults. In woolly monkeys, copulating pairs do not separate from the rest of the social group, and immatures appear to take an active interest in the copulations of associated adults. Two copulations between AFDs and BAMs were observed wherein associated juveniles attempted to come between their mothers and the BAM. Copulations have been observed being aggressively interrupted by other adult females in this population (Di Fiore and Schmitt, unpublished data), as well as at another nearby study site (Di Fiore 1997; Di Fiore and Fleischer 2005), but the intervention of associated juveniles appeared to be more playful than aggressive.

On one occasion in December 2007, an AFD in group Y with a JF1 still riding jockey-style copulated with a BAM while her juvenile was within 5 m playing. As intromission occurred, the JF1 approached and climbed onto the AFD's back, although the BAM was physically blocking its usual position, whereupon the JF1 grabbed the BAM in the face and appeared to try grappling with the BAM. In response, the BAM occasionally swiped and nipped at the JF1, and eventually dismounted from the AFD. Ejaculation could not be confirmed, although it was assumed at the time that the copulation was completed. On a second occasion, in group Y, a similar interaction occurred wherein a JF1, still mounted jockey-style on her mother, was successfully ignored by a copulating BAM. Although the JF1 made numerous vocalizations and moved around erratically on her mother's back, the BAM was unperturbed.

8.5.10 Dispersal and Related Behaviors

Three subadult females ("Audrey," "Figment," and "Sasha") disappeared from study groups shortly after beginning to show sexual interest in coresident BAMs and are presumed to have dispersed, and at least one subadult female ("Roosevelt") was suspected to have emigrated to group Y during the study period. At least two subadult males ("Lucifer" and "Vulcan") disappeared from group D, although their whereabouts are unknown, and there is compelling genetic evidence from another male ("Dante") in group D suggesting that he emigrated from the other side of the Tiputini river. Still, other behavioral observations suggest that woolly monkeys may deliberately peripheralize themselves from their social group within familiar home ranges, which, in tandem with extensively overlapping home ranges with other groups (Di Fiore and Schmitt, this volume; Schmitt et al. 2007) and relatively tolerant intergroup interactions, may allow for either codispersal to familiar groups or the formation of new social groups. For a more detailed discussion of predispersal behaviors at this study site, see Di Fiore et al. 2009.

8.6 Discussion

8.6.1 Life History Patterns

Understanding the long immature period in woolly monkeys is essential to gaining insight into the evolution of the relatively "long" life histories of atelins and other primates (Di Fiore & Campbell 2007; Stearns et al. 2003). The results of this study fit well with previous life history observations made in a longitudinal study of *L. lugens* in Colombia (Nishimura 2003). Woolly monkeys of both sexes appear to develop quickly both behaviorally and physically during the juvenile phase and reach locomotor independence around 2 years and social independence begins after 3 years with adolescence and subadulthood. Development appears to slow from the first signs of sexual maturity to dispersal or adulthood. The time immediately prior to and after reaching sexual maturity may be dramatically extended in *Lagothrix*. Further study focusing on this time period with more reliably identifiable individuals will be necessary to confirm this aspect of woolly monkey development.

8.6.2 Social Patterns

As in previous studies (e.g., Nishimura 1990a; Stevenson 1998), the patterns seen in juvenile woolly monkeys suggest that the most important social relationship during development is that between mother and offspring. On average, *Lagothrix* juveniles (and adults) rarely had more than one individual in proximity at all, and when they did, it was typically an adult female. Shifts in proximity throughout development seem to support this, with a significant drop in overall proximity levels being most likely explained by maternal independence. These patterns place the age categories of this study firmly within Nishimura's behaviorally defined age categories for *L. lugens* (Nishimura 1990a).

Also, as noted previously (Stevenson 1998), the drop in proximity noted in juvenile 2 individuals is consistent with observations that *Lagothrix* females with juvenile 2 offspring often appeared to have new infants. The birth of a sibling can have profound effects on the development and behavior of immature primates, typically increasing juvenile independence as maternal investment is reallocated to the new infant (e.g., Devinney et al. 2001, 2003; Berman 1992). Mothers with both infants and associated juvenile 2 individuals were often seen, but could not be differentiated due to problems with individual identification. Male woolly monkeys were generally more solitary than females. This pattern appears to develop gradually with age, as the number of individuals in proximity drops with each age grade.

Overall, these proximity patterns do not appear to strongly support the idea that juveniles preferentially interact with social partners that will be beneficial in the future given that juveniles, like adults, rarely associate with anyone outside of the mother–offspring relationship. The one exception noted—the apparent preference of SAMs for other adult males—suggests same-sex preferences in overall association patterns may not be important until the late juvenile phase or early adolescence. NN patterns provide more support for the idea that same-sex social preferences develop in the subadult phase, and males appear to spend a greater proportion of their time with adult males as their NNs as they age.

The preference for play between BAMs and juvenile males along with observations of grooming bouts, including extended grooming with mutual erections, between immature males and BAMs provides some evidence that adult males and juvenile males preferentially associate with each other in woolly monkeys, which is consistent with previous studies (Di Fiore 1997; Di Fiore and Fleischer 2005). Although these interactions are rare, given the overall rarity of social behavior generally in woolly monkeys, they could be of significant importance to the individuals involved. The high association of SAMs with other adult males may reflect an increased importance for male social bonding in younger, sexually mature males. Paired with anecdotal observations of restricted sexual behavior in SAMs, these results suggest that although sexual behavior among coresident males is generally tolerated in woolly monkeys (Nishimura 1990b; Nishimura 2003; Di Fiore and Fleischer 2005), such tolerance and access to sexual partners may be regulated in some way by coresident males. In such a case, the relatively high affiliation seen between adult and immature male woolly monkeys may be interpreted as an investment in future reproductive access within the group.

8.6.3 Subadulthood in Woolly Monkeys

The subadult phase of primate life histories is loosely defined as the period between the onset of sexual maturity and the assumption of fully adult social, physical, and reproductive roles (Pereira and Altmann 1985; Setchell and Lee 2004) and is perhaps even more poorly understood than the juvenile phase. The few studies on primates that have focused on subadult males have found dramatic developmental changes at work during this life history phase. In a long-term study of semi-free-ranging mandrills (*Mandrillus sphinx*), for example, male adolescence lasted from 4 to 10 years of age, and involved both dramatic behavioral changes in ranging patterns and associations with other groupmates and physiological changes such as increases in body mass, changes in fat distribution, and increased expression of male secondary sex characteristics (Setchell 2003; Setchell and Dixson 2002; Charpentier et al. 2004).

This extended subadult period in some taxa may be selected in several ways. Bercovitch (2000) found that in cercopithecid primates there was often a sex-based difference in not only the age at sexual maturity but also the length of time between the attainment of reproductive maturity and the actual onset of reproduction. Females in these taxa reach sexual maturity significantly earlier, while the observed onset of reproduction was significantly later in males. In all these taxa, there are high levels of competition between fully adult males paired with relative tolerance for immature-looking males. The subadult delay in male reproduction after sexual maturation, then, may be a relatively safe time in which comparatively small males can change both physiologically and socially, in order to more ably compete for matings (Setchell 2003; Charpentier et al. 2004). The bimaturism observed in orangutans (*Pongo* spp.) and mandrills takes this strategy a step further, in that it may represent cases in which the "adolescent" phase has been selectively lengthened and used as an evolutionarily stable alternative mating strategy alongside fully developed males (e.g., Utami and van Hoof 2004; Setchell and Lee 2004). In these cases, subadult males take advantage of full adult male tolerance for individuals that do not appear to be fully adult in order to sneak matings with—or force unwanted copulations upon—adult females. The subadult phase in female primates may also involve rapid growth (e.g., in *Gorilla*, Leigh 1992, 1995) and can involve reproduction prior to attainment of full adult stature or behavior (e.g., in *M. sphinx,* Setchell and Dixson 2001; in *Homo sapiens,* Bogin 1999).

Although woolly monkey males appear to be philopatric with relative tolerance for coresident males (Di Fiore and Fleischer 2005), there is some evidence that males may disperse (Di Fiore et al. 2009) and males have been observed to compete for matings with extra-group males for access to females during intergroup encounters (Schmitt, personal observation). Sexual dimorphism in body and canine size is well documented in this taxon (Schmitt and Di Fiore, in preparation; Di Fiore and Campbell 2007; Smith and Jungers 1997) and may represent adaptations to these forms of intrasexual competition. The extensive period from the Juvenile 2 phase to most markers of adulthood seen in *Lagothrix* may represent a phase of social and physiological development that may have its own selective mode (e.g., Pereira and Leigh 2003), similar to that seen in male mandrills (Setchell 2003; Setchell and Dixson 2002).

The apparent presence of a smaller adult male morph (defined as a SAM in this study) with behavior that is distinct from bigger adult males suggests that male adolescence, or at least subadulthood, in woolly monkeys may last much longer than is currently thought or defined in this study. The sample sizes of SAMs in this study are unfortunately small, with no more than one SAM per group, so a confident definition of this period is not currently possible. The scant evidence presented here, however, calls for a closer scrutiny of male behavior and development in this taxon up through the attainment of full BAM status. Larger sample sizes are needed to confidently detect whether SAM status could be considered a life phase that is truly distinct from other fully adult males or subsumed into a larger category of subadulthood. Recent research on male reproductive success at various ages in northern muriquis (*B. hypoxanthus*), wherein male reproduction was delayed a full 2 years after the first observed copulation, further suggests that the separation of younger adult males into a separate life history phase may be valid (Strier et al. 2011).

Large differences in adult female body size were also noted during this study, with some reproductive females being nearly 1.5 times as large as others (Schmitt and Di Fiore, in preparation). It is possible then that female *Lagothrix* may also face large physiological changes during the subadult phase and may reproduce prior to the attainment of full adult stature. Marked changes in female body size presumably take place after dispersal from the natal group, as young females who disappeared from our study group and who were presumed to have dispersed maintained lanky physiques and body sizes that were relatively small when compared to coresident reproductive females. Observations of dispersing females in *Brachyteles* suggest that dispersal occurs prior to sexual maturity (Strier and Ziegler 2000) and may significantly delay reproduction, as females typically did not begin reproducing until almost a year after their establishment in a new social group (Martins and Strier 2004). Female woolly monkeys (*L. lugens*) in Colombia may begin copulating earlier upon establishment in a new social group, but typically do not begin reproducing until roughly 3 years after initially dispersing (Nishimura 2003), and observations of multiple transfers between social groups before reproducing may increase the social and locational costs of dispersal (e.g., Isbell and Van Vuren 1996; Isbell and Young 2002). It is unclear whether this delay in reproduction after dispersal is due to not yet having attained sexual maturity or if there are social barriers to reproduction that must be negotiated (e.g., Drea 2005; Joffe 1997).

Although differences in body size among females are likely age based, observations of adult females aggressively interfering with the copulations of other adult females and male rejections of soliciting females suggest the possibility that these differences in body size may proffer some advantages in female intrasexual selection or male mate choice (Di Fiore 1997; Di Fiore and Fleischer 2005; Di Fiore and Campbell 2007; Schmitt and Di Fiore, unpublished data). It is possible that these aggressive copulations represent direct female–female competition for a male mate; however, females have not been observed to mate with the interrupted male, and previous work suggests that female woolly monkeys are rarely in estrus at the same time and may mate outside of conceptive periods (Nishimura 2003). Alternatively, immature appearance has been hypothesized to aid in limiting aggression from adult males in taxa with strong intrasexual male competition (Leigh 1995). It is possible that immature females disperse prior to attaining full adult stature in order to smooth over group integration, although the multiple adult dispersal events observed by Nishimura (2003) seem to counter this idea. Although individual subadult females can be difficult to identify in this species, and even more difficult to track once they have dispersed (but see Di Fiore et al. 2009; Nishimura 2003), information on behavior and development in this phase may be essential to understanding the selective pressures acting on delayed maturation and the delay in reproduction seen in *Lagothrix*.

8.7 Conclusions

This work gives us a small glimpse into the behavior and development of immature and adolescent woolly monkeys and demonstrates that there is room for future work along several intriguing lines of research. On the most basic level, longitudinal studies of juveniles and subadults in woolly monkey populations where individual identification is reliably possible are necessary for a more nuanced understanding of juvenile behavior and development in this genus. In line with Nishimura's previous work on life history in woolly monkeys, populations of *L. lugens* in Colombia may be ideal for these purposes, as adult females are identifiable by both clitoral and facial pigmentation (Pablo Stevenson, personal communication). However, potential variation across taxa within *Lagothrix* should not be ignored. Building on our own work here, with an ever-increasing number of individuals with external identification markers so that numerous identifiable infants can be followed from birth, TBS will also be an excellent site for longitudinal work. For the purposes of better characterizing rare behavioral patterns, such as nursing and finer patterns of infant independence, all-day follows of identifiable focal animals should be incorporated into future studies.

Closer follows of individual life histories are also necessary, in both males and females, from sexual maturity to establishment as full adult individuals. Both the presence of the behaviorally and morphologically distinct SAMs and the extensive time before first reproduction in adolescent females mark this life history phase as one of particular interest and potential import within the genus *Lagothrix*. Studies in other atelin taxa show a surprising variety in the paths that adolescents take to adulthood, from remaining in their natal group (in both sexes, albeit more rarely for females) to dispersal and later establishment (e.g., Printes and Strier 1999; Martins and Strier 2004; Campbell 2003; Vick 2008). Direct comparisons with other atelins with comparable datasets could also better illuminate taxonomic patterns within the Atelini, and help reveal how intergeneric variation may complicate our view of how conservative and variable juvenile life histories may be across taxonomic space.

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Chapter 9
Seed Dispersal by Woolly Monkeys (*Lagothrix lagothricha*) at Caparú Biological Station (Colombia): Quantitative Description and Qualitative Analysis

Marcos González and Pablo R. Stevenson

Abstract Seed dispersal is considered to play a fundamental role in the maintenance of tropical forest structure and diversity. The aim of this study was to determine the role that woolly monkeys play as seed dispersers at the Caparú Biological Station. We followed two woolly monkey groups for 16 months (960 h of observations), determined their diet, and collected and analyzed 1,397 fecal depositions. In 99 % of the analyzed depositions, we found seeds (93,917 seeds) belonging to at least 118 plant species. We estimated that an individual defecates around 15 times per day, and that the woolly monkey population can disperse more than 6,822 seeds day^{-1} km^{-2}. However, if corrected for sampling efficiency, this value can reach 70,100 seeds day^{-1} km^{-2}. The vast majority of seeds that woolly monkeys ingest are dispersed whole and undamaged. The average retention time was around 10 h, and the mean dispersal distance was 577 m (range 0–1, 540 m, $N=66$). Germination experiments using dispersed seeds show higher (or equal) germination rates and shorter (or equal) latency times for dispersed seeds compared to controls. Our results confirm the important ecological role that woolly monkeys play in tropical forests and also show that this role depends to a great extent on population densities.

Keywords Germination rates · Seed dispersal effectiveness · Dispersal quantity

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M. González (✉)
Centro de Investigaciones Ecológicas La Macarena, Departamento de Ciencias Biológicas,
Universidad de Los Andes, Bogotá, Colombia
e-mail: marcosdelcocuy@gmail.com

P. R. Stevenson
Departamento de Ciencias Biológicas, Universidad de los Andes,
Bogotá, Colombia
e-mail: pstevens@uniandes.edu.co

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9.1 Introduction

Seed dispersal, understood as the displacement of seeds away from the parent tree, has profound effects on the survival and recruitment of seedlings and spatial distribution of adult plants and is also a key factor in the maintenance of diversity in tropical forests (Webb and Peart 2001; Terborgh et al. 2002; Nuñez-Itauri et al. 2008; Stevenson 2011). Studies on Neotropical plants have demonstrated that plants have a higher chance of recruitment and survival when dispersed far from the parent tree and conspecifics (Clark and Clark 1984; Wills et al. 1997; Stevenson 2007a; Terborgh et al. 2002; Swamy and Terborgh 2010; Swamy et al. 2011). Janzen (1970) and Connell (1971) stated that the high density of seeds and seedlings near parent trees attracts predators, increases the probability of infestation with plagues, and intensifies intraspecific competition. All these lead to a reduction in survival for individual seeds and seedlings near parent trees. It has also been suggested that seed dispersal, besides helping to disperse seeds into areas of reduced density-dependent mortality, has the advantage of allowing the colonization of adequate habitats for establishment (Howe and Smallwood 1982).

In tropical ecosystems, endozoochorous dispersal (seeds that are swallowed and then defecated by animals) is the most common way in which plants disperse their seeds. Between 50 and 90 % of woody plants are dispersed by frugivorous vertebrates, and most woody plants have fruits with morphological traits (e.g., fleshy fruits) that are associated with the facilitation of dispersal by animals (Frankie et al. 1974; Howe and Smallwood 1982; Janson 1983; Gautier-Hion et al. 1985; Fleming et al. 1987; Tabarelli and Peres 2002; Link and Stevenson 2004). However, producing fleshy fruits does not guarantee seed dispersal, since some animals consume fruits without dispersing their seeds. This occurs when seeds are not swallowed, fruits are consumed unripe (before seeds are viable), seeds are damaged, or when animals prey upon seeds (Lambert and Garber 1998; Norconk et al. 1998). As a consequence, the effectiveness of a disperser can be measured in terms of quantity (the number of seeds it disperses) and quality (Schupp 1993; Schupp et al. 2010). The quality of dispersion is associated with factors such as the distance at which seeds are dispersed and the treatment that seeds receive (i.e., degree of predation, viability of seeds after gut passage), and conditions in which they are deposited.

Primates from the Atelinae subfamily have been recognized as some of the most important seed dispersers in Neotropical forests (Chapman 1989, 1995; Andresen 1999; Stevenson 2000, 2007b; Dew 2005; Russo et al. 2005; Link and Di Fiore 2006; Palma and Stevenson 2010). Their role as seed dispersers is a result of their large body size, large home ranges, and long daily traveled distances (Defler 2004; Stevenson et al. 2000; Gonzalez and Stevenson 2010), which allow them to consume a large quantity of fruits and take their seeds far from the parent tree. However, it is still not possible to generalize the role of woolly monkeys as seed dispersers, since only a few populations have been quantitatively described.

The aim of this study was to determine the role of woolly monkeys (*Lagothrix lagothricha lagothricha*) as seed dispersers in the Caparú Biological Station (Vaupés, Colombia). To achieve this, we performed a quantitative estimation of seed dispersal by woolly monkeys based on the number of seeds and the daily dispersed biomass, and we established which plant species were dispersed and in what proportions. To obtain an indicator of the quality of dispersal we studied three parameters: (1) treatment of seeds (i.e., preyed, spitted, consumed unripe, chewed); (2) dispersal distance; and (3) germination rates of dispersed and undispersed seeds. Gathering this information is important because the extinction of seed dispersers dramatically affects regeneration patterns and, in the long term, alters forest composition and reduces forest diversity (Peres and van Roosmalen 2002; Nuñez-Itauri et al. 2008; Stevenson 2011). This matter is of special interest if we consider that atelines are species particularly vulnerable to habitat loss and hunting (Alvard et al. 1997; Peres and Palacios 2007).

9.2 Methods

9.2.1 Study Area

The Caparú Biological Station (also known as Mosiro Itajura) is located at the southeast of the Vaupés department, Colombia, near Lake Taraira, an ancient meander of the Apaporis River (69° 31′ W and 1° 04′ S, ca. 200 m; Defler 1999). The station is located on a terrace of Pleistocene origin and includes five different forest types (Fig. 9.1). The warm super-humid climate has a slightly bimodal rain regime (Rangel and Luengas 1997) with an average yearly precipitation of 3,950 mm (Defler 1996). The month of maximum precipitation is May (425.7 mm), while the driest month is September (257 mm; Palacios et al. 2009). The average yearly temperature is 25.1 °C with slight variations throughout the year, and soils are generally shallow and acidic with low fertility (Defler 1996). Fruit abundance varies considerably during different months of the year, between years, and across forest types (Defler and Defler 1996; Vargas and Stevenson 2009; Gonzalez and Stevenson 2010). For instance, during our study period, the lowest fruit production was observed between October and January and the highest peak in fruit production was during April and May. However, the general estimated fruit supply is relatively low at 106–394 kg ha^{-1} yr^{-1} (Vargas and Stevenson 2009; González and Stevenson 2010).

9.2.2 Study Groups

In Caparú, woolly monkeys (*L. l. lagothricha*) are the largest primate species, weighing up to 7–9 kg (Defler 1999). Their diet is composed primarily of fruits, supplemented with arthropods, leaves, and other minor items (Defler and Defler 1996; Gonzalez and Stevenson 2010). At least four groups were observed in the trail system, two of which we studied (Selección Colombia and Futbol Club Barcelona).

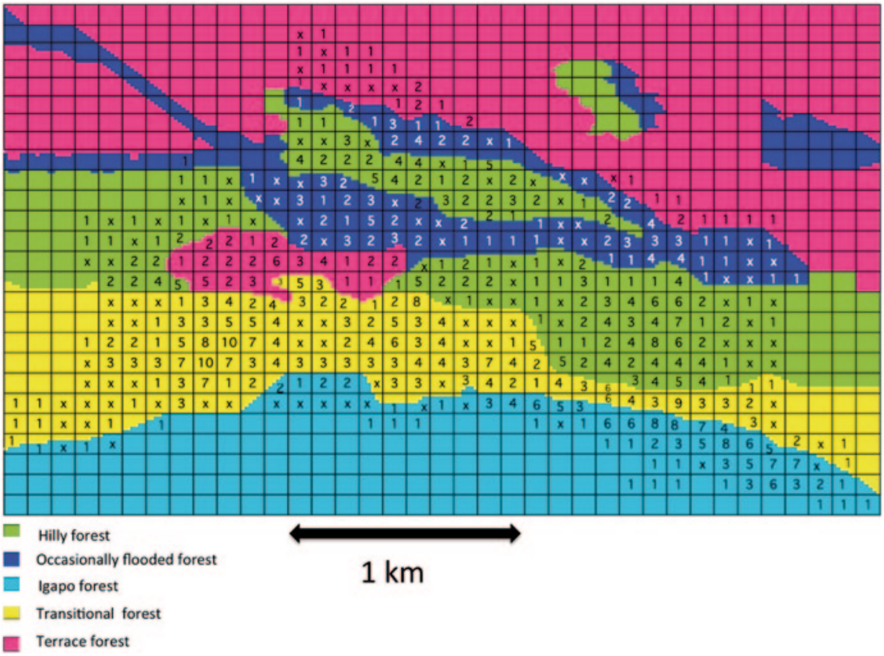

Fig. 9.1 Home range of the main study group of woolly monkeys at the Caparú Biological Station, Vaupés (Colombia), superimposed on the map of forest types. Each quadrant represents 1 ha (modified form Defler and Defler 1996). The numbers represents the number of days in which the troop was observed in each hectare (using the position data registered every 30 min). *X* means that the monkeys used the quadrant for displacement but position data were not recorded

Group SC accounted for 84 % of our observations and was a large group of about 40 individuals. In this group, we identified at least 4 adult females with dependent infants, 15 adult males, and 11 adult females without dependent young. Group FCB was a smaller group consisting of 15 individuals, including 2 females with dependent infants, 3 adult males, and 1 adult female without dependent young.

9.2.3 General Field Protocol

We followed focal woolly monkeys for 5 full (i.e., 12 daytime hours) days per month between March 2004 and June 2005 (960 h total). Using a compass and the trail system as reference, we delineated the route of the group on a map (1:12, 500 scale), and then estimated daily path length (DPL) using a map measurer. We recorded the position of the troop within the home range every 30 min on a grid of hectare plots (Fig. 9.1).

We were unable to recognize all individuals in our study groups; therefore, it was impossible to follow a protocol to choose focal animals. In general, when a focal animal was lost we followed another animal in our proximity. We recorded the duration of all feeding bouts when the monkeys were observed feeding on ripe fruits, unripe fruits, leaves, and flowers (Stevenson et al. 1994). When monkeys fed on fruits, we noted whether seeds were swallowed, spat, or preyed upon. The location of the trees visited was registered and mapped relative to a trail system marked every 50 m.

9.2.4 Fecal Samples

We collected a total of 1,397 fecal samples. Most samples came from the focal individual, but for some analyses we included depositions from other individuals. We defined a fecal sample as the fecal matter deposited by an individual in a particular place, during a period of 1 min. For every sample produced, we registered the time and exact location at which the fecal sample was collected and the sex and age class of the individual whenever possible. Since woolly monkeys occupy the higher strata of the forest, defecations are often scattered by intervening vegetation when dropping to the ground. Therefore, the time destined to search for each deposition has a great influence on the proportion that is recovered. To avoid this bias, we searched for each deposition for a maximum of 5 min (Stevenson 2002). Depositions were washed individually using a 1 mm sieve, and all seeds were identified to the lowest possible taxonomic level. Seeds were counted individually or, for the smaller seeds (≤3 mm *Ficus* y *Cecropia*), their number was estimated. Seeds were classified as undamaged, when we found the entire seed, or as predated seeds, when we found masticated pieces of seed. Any recognizable fragment of a seed was considered as having been preyed upon as part of the diet of that animal. We additionally dried and weighted 10 seeds of each species to determine their dry mass and, thus, estimate the dry biomass dispersed by woolly monkeys.

Germination Rate and Dormancy Time Germination experiments were conducted using between 24 and 125 seeds of the 12 most common species in the fecal samples (Table 9.2). For these experiments, seeds were carefully washed and placed in pots with soil. As controls, we used seeds picked up from below the parent plant and cleaned.

Dispersal Distances and Retention Times Defecated seeds that could be assigned to a specific parent plant were used as markers to estimate gut passage times and dispersal distances. To obtain valid data and minimize the probability of incorrectly assigning a defecated seed to an incorrectly identified parent tree, we followed similar criteria used by Stevenson (2000), Russo (2003), and Link and Di Fiore (2006). To assign a parent to a seed, it had to satisfy the following two requirements: First, the monkeys fed from only one particular individual of the species assigned to a defecated seed during the sampling period (if the monkeys feed on the same individual feeding patch several times, we used these data for estimating dispersal distance but not retention times). If more than one tree of the same species was visited, it was impossible to estimate the dispersal distance or retention times using seeds as markers. Second, seeds from that species were defecated for the first time at least 3 h after the beginning of the observations. This last criterion was designed to minimize the probability of wrongly assigning the location of a tree visited during the focal animal sample, when the seeds actually were swallowed before focal sampling began. Long focal follows are recommended to get precise dispersal distance estimates (Stevenson 2000), but this was not possible in the present study. Fitting the criteria, we could only determine the dispersal distance for 2.1 % (212) of the large seeds (>3 mm), and never for seeds of ≤3 mm. To avoid pseudoreplication, when a deposition contained more than one seed from the same parent tree, we took the deposition as a single dispersal distance. In those cases in which two depositions, containing seeds from the same parent tree, were excreted by different individuals in the same place (typical of resting periods at midday), we used only the first deposition. In total, we obtained 66 dispersal distance estimates.

9.2.5 Statistical Analysis

We used regression analysis to predict the mass of dispersed seeds from two potential variables: (1) fruit production in the forest (as measured by Gonzalez and Stevenson 2010) and (2) consumption time during observations. We used a one-way analysis of variance to examine differences in the mass of dispersed seeds between four different age/sex classes. We used Spearman's correlation analysis to evaluate the relationship between retention time and seed dispersal distance. To compare the association between the probability of germination and whether seeds were dispersed or not, we performed a G-test (Sokal and Rohlf 1995) using the Pop Tools software for Excel. To compare germination times between dispersed and non-dispersed seeds, we performed a Mann–Whitney test, using SPSS 12 for Windows.

9.3 Results

9.3.1 Dispersal Quantity

We collected a total of 1,397 depositions and we found seeds in 99 % of them. We found that the depositions contained 93,917 seeds, of which 89 % (83,829) corresponded to small seeds of less than 3 mm diameter (i.e., *Ficus* spp. and *Cecropia* spp.). However, in terms of biomass, large seeds (>3 mm) comprised the vast majority (Table 9.1).

The estimated seed biomass per deposition was of 3.7 ± 3.3 g. However, the range was very wide: from 0 g in those cases in which depositions did not contain seeds (1 %) to 23.3 g in one single deposition. This variation was associated with the seasonality of the fruit availability for this forest ($R^2 = 0.46$, $P = 0.016$, $N = 12$).

Table 9.1 Characteristics of an average woolly monkey deposition at Caparú.

	Number of seeds	Number of seed >3 mm	Biomass of seeds (dry gr)	Biomass of seeds >3 mm (dry gr)	Number of species
Average	68.0	7.6	3.7	3.8	2.4
SD	243.4	11.2	3.3	3.4	1.3
Range	0–3,505	0–187	0–23.3	0–19.4	0–9
Number of fecal samples	1,397	1,341	1,397	1,341	1,397

Biomass estimations correspond to dry biomass values, and were obtained from an average of several seeds of each species

We found higher dispersed biomass values between March and May, showing high productivity (4.6 gr ± 1.4 standard deviation, SD), and lower values between November and January, the fruit scarcity period (1.60 gr ± 0.59 SD).

There were no significant differences in the size of depositions among sex–age classes ($F=0.42$; df=3, $P=0.74$). Correcting for sampling time biases, we estimated that a woolly monkey excretes around 15 times per day (excluding night hours when they were not observed). Using these data and the mean value for the number of seeds per defecation, we estimated that individual woolly monkeys dispersed an average of 1,034 seeds per day, including 116 seeds >3 mm. Given a population density of 6.6 individuals km^{-2} in the study area (Palacios and Peres 2005), woolly monkeys disperse ≈6,822 seeds day^{-1} km^{-2} and ≈762 seeds (>3 mm) day^{-1} km^{-2}. However, this is a highly conservative estimate, since it assumes a collection efficiency of 100%, and does not take into account night depositions. Using the corrections suggested by Stevenson (2007b), which consider these two factors, we estimated that woolly monkeys at Caparú disperse ≈70,100 seeds day^{-1} km^{-2}, including ≈2,940 seeds >3 mm day^{-1} km−2.

Our results indicate that woolly monkeys at Caparú disperse at least 118 fruit species (Appendix 9.1). In cases in which it was not possible to classify seeds to the species level (i.e., seeds of the *Ficus* and *Inga,* and some seeds from the Moraceae and Sapotaceae families), we assumed that seeds belonging to one of these groups corresponded to a single species. This clearly underestimates the number of dispersed species, especially since in this locality these taxa are represented by more than 30 species (Clavijo. unpubl. data). Even more, Defler and Defler (1996) reported the consumption by woolly monkeys of at least 30 species of Sapotaceae, and 31 of Moraceae. Additionally, there are several species that are consumed in very low quantities, which reduces the chance of finding their seeds in the feces.

Even though the diversity of dispersed seed species is very high, a large percentage of the dispersed biomass corresponds to a few genera and families. In terms of seed numbers, *Cecropia* and *Ficus* species represent 89% of the total number of seeds. Similarly, five species represent 39.8% of the dispersed biomass—*Dicranostyles ampla* (570 g, 11%), *Telitoxicum krukovii* (526 g, 10.2%), *Parkia multijuga* (473 g, 9.2%), *Iriartea deltoidea* (297 g, 5.7%), and *Pouteria vernicosa* (190 g, 3.7%); and four families represent 55.3% of the dispersed biomass—Sapotaceae (754.7 g, 15%), Convolvulaceae (745 g, 14%), Menispermaceae (687.7 g, 13%), Fabaceae–Mimosoideae (669.6 g, 13%).

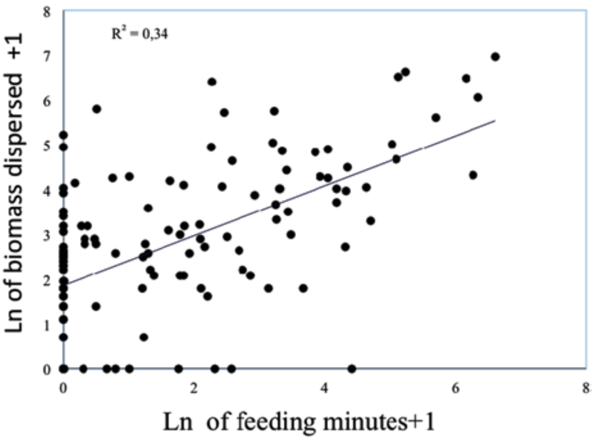

Fig. 9.2 Correlation between fruit consumption time and the mass of dispersed seeds by the population of woolly monkeys at the Caparú Biological Station, Vaupés, Colombia

9.3.2 Dispersal Quality

We found that woolly monkeys swallowed seeds from almost all of the species they ate. We found a positive correlation between the time of consumption of each species and the dispersed biomass ($R^2 = 0.34$, $P < 0.001$, $N = 127$; Fig. 9.2). For only three species (*Caryomene foveolata*-consumption time = 29 min, *Iryanthera crassifolia* = 2 min, *Astrocaryum aculeatum* = 2 min), we observed woolly monkeys spitting or destroying the seeds rather than swallowing them. The largest seeds found in this study were 17.6 mm (*Curarea toxicofera*) and 18.3 mm wide (*Salacia aff. elliptica*).

In most cases, woolly monkeys fed on ripe fruits. However, in a few cases (2.3 % of total feeding time), individuals were observed feeding on unripe fruits and preying upon their seeds. Nevertheless, four out of the six species that were consumed unripe were also consumed ripe and their seeds were ingested whole, in a much higher proportion than the one in which they consume unripe fruits (996 vs. 37 min). In almost all cases, woolly monkeys swallow seeds whole, without biting or chewing them. In the 1,397 analyzed depositions, we found 93,917 complete seeds and only 25 chewed or damaged seeds, which corresponds to 0.2 % of the total of large seeds found.

The average dispersal distance for seeds was 577 ± 361 m SD, and some seeds were dispersed up to 1,540 m from their original source. Of the 66 cases for which dispersal distance was determined, 87 % were dispersed at distances of more than 100 m, and only 5.7 % were excreted at less than 50 m from the parent tree. Almost all of the seeds (18 of 27) that were dispersed at less than 100 m belong to a single individual of *Eugenia florida,* which was used by the woolly monkeys in several occasions as a dormitory during 1 month. The mean duration of seeds passing through the digestive tract was 10 h 4 min (range, 2 h 31 min to 26 h 53 min, $n = 20$). There was no relation between retention time and the distance at which the seeds were dispersed ($r_s = 0.0024$, $P = 0.49$, $N = 42$).

Table 9.2 Comparison of the germination percentage and latency time of dispersed and undispersed seeds by woolly monkeys at Caparú. In the first column, the number of seeds used in each experiment

Species Family (Dispersed/ Undispersed)	Time (days) of latency (Dispersed/Undispersed)	Percentage of germination (Dispersed/Undispersed)
Pouteria vernicosa	14/19	81/56
Sapotaceae (80/80)	(U=965; P=<0.01)	(G=11.7; P=<0.01)
Telitoxicum krukovii	20/27	96/89
Menispermaceae (112/57)	(U=688; P=<0.01)	(G=2.9; P=0.09)
Brosimum lactescens	60/64	90/67
Moraceae (40/40)	(U=344; P=0.04)	(G=6.1; P=0.01)
Pleurisanthes cf. emarginata	25/29	96/87
Icacinaceae (24/24)	(U=123; P=<0.01)	(G=1.0; P=0.31)
Coccoloba excelsa	13/18	73/70
Polygonaceae (48/50)	(U=255; P=<0.01)	(G=0.2; P=0.63)
Pouteria aubrevillei	22/15	67/51
Sapotaceae (125/125)	(U=264; P=0.62)	(G=5.5; P=0.02)
Eugenia florida	48/49	70/52
Myrtaceae (50/50)	(U=417; P=0.57)	(G=3.4; P=0.07)
Parkia multijuga	94/87	29/19
Fabaceae (100/100)	(U=250; P=0.59)	(G=2.8; P=0.09)
Buchenavia grandis	84/75	79/39
Combretaceae (33/33)	(U=108; P=0.06)	(G=10.7; P=<0.01)
Sorocea pubivena	9/11	60/78
Moraceae (50/50)	(U=416; P=0.04)	(G=3.8; P=0.05)
Virola pavonis	101/44	17/45
Myristicaceae (60/40)	(U=45; P=0.03)	(G=9.3; P= <0.01)
Dicranostyles ampla	9/11	96/90
Convolvulaceae (100/50)	(U=1881; P=0.20)	(G=1.9; P=0.17)

The first column shows the number of seeds used in each experiment

In 7 out of the 12 plant species, seeds that had passed through the digestive tract (dispersed) germinated significantly faster than controls. One showed the opposite pattern, and in four cases there were no differences between the treatments. The experiments in which we estimated the percentage of germination offered similar results—seven showed significant differences indicating that the percentage of germinated seeds was higher when these pass through the digestive tract; two showed the opposite pattern (higher percentage of germination for seeds which have not passed through the digestive tract); and three did not show significant differences between treatments (Table 9.2).

Table 9.3 Data on dispersal of large seeds (>3 mm) by three ateline taxa, reported by different studies

Study	Species	Number of seeds/deposition^{-1}	Number of depositions/day^{-1e}	Dispersed seed km^{-2} day^{-1}
Gonzalez and Stevenson[a]	*L. l. lagothricha*	7.6	15.2	762
Dew[b]	*L. l. lagothricha*	3.2	5.8	575
Stevenson[c]	*L. l. lugens*	11.9	13	8,060
Dew[b]	*A. belzebuth*	3.4	7	274
Link and Di Fiore[d]	*A. belzebuth*	7.8	13.7	738

[a] This study
[b] Dew 2005
[c] Stevenson 2007b
[d] Link and Di Fiore 2006
[e] Days of 12 daytime hours

9.4 Discussion

9.4.1 Dispersal Quantity

Previous studies have quantified the number of seeds dispersed by atelines (Stevenson 2000, 2002, 2007b; Dew 2008; Link and Di Fiore 2006; Palma and Stevenson 2010; Table 9.3). This study confirms that the role as efficient seed dispersers is common to all the ateline populations studied so far. Consequently, woolly monkeys seem to play a similar ecological role wherever they have been studied. However, estimates at the population level are largely different among localities, and differences are mainly due to the fact that non-abundant populations do not disperse as many seeds. The important role of atelines as efficient seed dispersers suggests that the reduction or extinction of their populations can cause important changes on the plant community.

Similar to what has been reported previously, we found that the majority of fruit species consumed by woolly monkeys are dispersed in quantities proportional to the time of consumption (Fig. 9.2). There are only some exceptions, and these correspond to fruits with seeds that are too large (in width), and others where individuals tend to be preyed upon when fruits are unripe.

There are morphological restrictions in the maximum size of seeds that an animal can swallow and, thus, disperse endozoochorously. Dew (2008) proposed that the maximum size that a seed could have for it to be swallowed whole by a woolly monkey, was 17 mm in its second highest dimension (width). Similarly, Stevenson et al. (2005) found seeds of up to 18 mm in width in *L. l. lugens* feces. These results support the idea that woolly monkeys have morphological restrictions that prevent them from dispersing seeds larger than 20 mm wide. Dew (2008) reported that for *Ateles belzebuth* this restriction is lower, allowing them to disperse larger seeds (up to 27 mm in width). As a result, there are species that can be dispersed by *Ateles* but not by *Lagothrix*. This is of ecological importance because it shows that, despite the similarities between these two genera, they play slightly different ecological roles.

There are species that show a high consumption time, but were not dispersed by woolly monkeys. This was the case of the autochorous *Micrandra spruceana,* one of the most abundant species in Caparú (Cano and Stevenson 2009). Woolly monkeys consume *M. spruceana* fruits when they are unripe, a state in which the maturing husk contains high quantities of latex, while the maturing seed is eatable when removed from the husk, which the woollies handily accomplish with a bite. The fact that woolly monkeys consume *M. spruceana* seeds in high quantities does not seem to be associated with a low fruit offering ($R^2=0.004$, $P=0.54$, $N=12$). Therefore, it is probable that this species represents an important nutritional complement in the diet of woolly monkeys. Although mature *M. spruceana* seeds are considered highly poisonous by local indigenous people (i.e., Tanimuca and Yucuna etnias, perhaps because of accumulated tannins). Mature seeds of this species were formerly eaten by indigenous people as a source of starch after processing them by crushing and washing them liberally with water, suggesting that soluble chemical defenses accumulate during maturation (Defler pers. communication).

9.4.2 Dispersal distance

Of the 212 seeds for which dispersal distance was calculated, 184 (86.8%) were dispersed at distances more than 100 m, and only 12 seeds (5.7%) were dispersed less than 50 m from the parent tree. Similar patterns have been reported for other woolly monkey populations and other ateline species. Stevenson (2002) estimated that only 1.1% of the seeds excreted by woolly monkeys at Tinigua Park, fell less than 15 m from the parent tree. Likewise, Link and Di Fiore (2006) estimated that 85.4% of the seeds defecated by *A. belzebuth* were deposited at more than 100 m from the parent tree, and only 2.1% were defecated at less than 20 m or less. These data show that almost all of the seeds dispersed by atelines are taken far from their source, enabling them to escape the distance and density-dependent effects that affect individuals near parent trees (Wills et al. 1997; Hubbell et al. 2001; Swamy and Terborgh 2010). Although we did not quantify the proportion of dispersed seeds that land below conspecific crowns, we think that it must be low. This proportion of dispersed seeds was estimated in Tinigua Park as 6%, and tree diversity is higher in Caparú than in Tinigua, suggesting that this proportion should be even lower in Caparú.

The distances at which woolly monkeys dispersed the seeds at Caparú are the largest reported for atelines so far (Julliot 1996; Dew 2005; Stevenson 2002; Link and Di Fiore 2006; Palma and Stevenson 2010). This seems to be due to the particularly long and relatively straight distances traveled by woolly monkeys at Caparú (Gonzalez 2007; Gonzalez and Stevenson 2010) and the large home-range size (Fig. 9.1). Previous studies (Defler 1996; Defler and Defler 1996; González and Stevenson 2010; Vargas and Stevenson 2009) had suggested that the low fruit availability at Caparú with marked periods of scarcity forces woolly monkeys to have long daily travel distances and large home ranges, compared to other populations and species of atelines. In fact, there is a negative correlation between fruit availability and the degree of straightness of the traveled paths and a positive correlation between the latter and dispersal distance (Gonzalez 2007). This suggests that, in periods of fruit scarcity, woolly monkeys travel longer and straighter paths and, as a consequence, disperse seeds at larger distances.

9.4.3 Germination Rates

The germination experiments indicate that passing through the digestive tract of woolly monkeys generally does not negatively affect seeds, since these maintain their capacity to germinate after being swallowed and excreted. Similar results were reported by Dew (2005) and Stevenson et al. (2002). However, in these experiments seeds were washed, and traces of feces (in the case of the dispersed seeds) or pulp (in the case of the non-dispersed) were removed. The fecal matter that covers the seeds when they are dispersed and the pulp that primates remove from them when consuming the fruits may have important effects on germination rates. It has been suggested that removing the pulp and the seed coat is one of the important tasks that woolly monkeys perform when dispersing the seeds (Liu et al. 2004). Additionally, the feces covering dispersed seeds increase the probability of secondary dispersal by beetles and at the same time reduces the chances of predation by rodents when seeds are buried (Andresen and Feer 2005). Thus, future studies intending to evaluate the effect of dispersal by primates on seed germination rates should consider these two factors.

Overall, our comparisons support the idea that different populations of woolly monkeys play a very similar role as seed dispersers, despite the differences in the flora and local conditions among the sites where they have been studied. In order to maintain forest diversity and the ecological processes associated with seed dispersal by atelines, and considering that their effect depends to a great extent on the abundance of their populations, it is of great importance to protect these primates

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Appendix 9.1

Species dispersed by woolly monkeys at Caparú. The biomass (dry seeds), the number of seeds, and the quantity of feces found for each species is shown. The number of visits and total time of consumption are also shown. The species are ordered in terms of mass of dispersed seeds because, in spite that seeds are potential individuals, in continuous forests there is a stronger correlation between the mass of seeds dispersed and the abundance of seedlings than between the number of seeds dispersed and seedling abundance (Stevenson, unpublished).

Species	Family	Life form	Biomass (gr)	Number of seeds	Number of feces	Number of visits	Number of minutes
Dicranostyles ampla	Convolvulaceae	Liana	570	1326	191	29	425
Telitoxicum krukovii	Menispermaceae	Liana	526	163	76	9	74
Parkia multijuga	Fabaceae	Tree	473	408	170	46	655
Iriartea deltoidea	Arecaceae	Palm	297	144	89	77	267
Pouteria vernicosa	Sapotaceae	Tree	190	109	56	17	225
Maripa janusiana	Menispermaceae	Liana	167	167	58	30	671
Buchenavia grandis	Combretaceae	Tree	127	63	28	2	36
Pleurisanthes cf. emarginata	Icacinaceae	± Tree	109	139	41	4	26
Strychnos panurensis	Loganiaceae	Tiana	102	148	42	11	56
Pouteria campanulata	Sapotaceae	Tree	97	81	39	8	139
Pouteria aubrevillei	Sapotaceae	Tree	90	199	58	3	55
Minquartia guianensis	Olacaceae	Tree	83	64	29	0	0
Cecropia sciadophylla	Urticaceae	Tree	76	40,549	285	27	88
Coccoloba excelsa	Polygonaceae	Liana	74	80	38	4	52
Telitoxicum minutiflorum	Menispermaceae	Liana	74	60	23	2	14
Hymenaea oblongifolia	Fabaceae	Tree	65	17	8	4	54
Cheiloclinium hippocrateoides	Celastraceae	Liana	63	48	18	21	83
Pseudolmedia rigida	Moraceae	Tree	57	297	31	7	69
Virola pavonis	Myristicaceae	Tree	56	38	23	12	133
Pourouma bicolor	Urticaceae	Tree	50	85	41	22	72
Pouteria sp. 2 (L. C-R 1081)	Sapotaceae	Tree	46.5	55	26	5	36
Eugenia florida	Myrtaceae	Tree	46.4	80	26	8	125
Pouteria laevigata	Sapotaceae	Tree	40	11	6	3	53
Virola elongata	Myristicaceae	Tree	38	55	13	1	5
Inga edulis	Fabaceae	Tree	32	79	13	26	294

Species	Family	Life form	Biomass (gr)	Number of seeds	Number of feces	Number of visits	Number of minutes
Clarisia racemosa	Moraceae	Tree	31	17	9	4	19
Paullinia sp. 1 (M. G 9)	Sapindaceae	Liana	29.9	22	11	4	32
Paullinia sp. 2 (L.C-R 1086)	Sapindaceae	Liana	29.6	80	31	12	83
Byrsonima cowanii	Malpighiaceae	Tree	27	83	23	13	128
Dialium guianense	Fabaceae	Tree	26.6	133	42	3	54
Brosimum lactescens	Moraceae	Tree	26.1	90	40	12	54
Couma macrocarpa	Apocynaceae	Tree	25.2	28	11	4	27
Odontocarya emarginata	Menispermaceae	Liana	24.7	76	16	6	38
Byrsonima arthropoda	Malpighiaceae	Tree	24.2	485	51	20	310
Strychnos mitscherlichii	Loganiaceae	Liana	23	29	12	25	153
Anomospermum (M. G. 51)	Menispermaceae	Liana	22	8	8	1	5
Sapotaceae sp. 3 (I.N. 11)	Sapotaceae	Tree	21.6	18	13	1	3
Buchenavia sp. (L. C-R 476)	Combretaceae	Tree	19.5	13	3	3	20
Curarea toxicofera	Menispermaceae	Liana	17.8	8	6	6	47
Chrysophyllum amazonicum	Sapotaceae	Tree	17.3	34	15	5	65
Pouteria guianensis	Sapotaceae	Tree	16.9	10	6	3	7
Talisia obovata	Sapindaceae	Tree	16.6	26	10	2	7
Protium cf. llanorum	Burseraceae	Tree	16.1	27	15	8	72
Roucheria columbiana	Linaceae	Tree	15.8	77	22	3	8
Batocarpus orinocensis	Moraceae	Tree	13.6	20	5	3	13
Micropholis venulosa	Sapotaceae	Tree	13.1	32	13	3	25
Protium cf. apiculatum	Burseraceae	Tree	12.5	39	16	8	166
Hebepetalum humiriifolium	Linaceae	Tree	12.2	55	11	10	102
Crepidospermum rhoifolium	Burseraceae	Tree	12.15	27	8	3	25
Guatteria insculpta	Annonaceae	Tree	12.1	11	7	0	0

Species	Family	Life form	Biomass (gr)	Number of seeds	Number of feces	Number of visits	Number of minutes
Sapotaceae sp. 4 (I.N.V 13)	Sapotaceae	Tree	12	10	7	11	275
Tontelea mauritioides	Celastraceae	Liana	11.5	10	3	7	34
Helicostylis tomentosa	Moraceae	Tree	11.2	25	12	6	18
Sorocea pubivena	Moraceae	Tree	10.6	71	28	15	301
Guatteria cf. olivacea	Annonaceae	Tree	10.3	24	5	6	57
Tapirira guianensis	Anacardiaceae	Tree	9.1	13	10	0	0
Ficus spp.	Moraceae	Trees and hemiepiphytes	8.7	43,280	270	42	599
Virola cf. duckei	Myristicaceae	Tree	8.6	5	2	17	140
Touroulia amazonica	Ochnaceae	Tree	8.1	45	7	2	4
Salacia aff. elliptica	Celastraceae	Liana	7.7	2	2	3	14
Odontocarya petiolaris	Mensipermaceae	Liana	7.2	20	11	1	5
Alibertia edulis	Rubiaceae	Tree	7.1	146	29	3	17
Guatteria foliosa	Annonaceae	Tree	7.06	107	46	7	24
Inga acreana	Fabaceae	Tree	6.9	23	4	8	38
Pouteria cf. bilocularis	Sapotaceae	Tree	6.5	5	4	1	14
Pouteria sp. 1 (L.C-R 917)	Sapotaceae	Tree	6.15	5	3	1	13
Protium amazonicum	Burseraceae	Tree	6.09	21	11	8	85
Inga tenuistipula	Fabaceae	Tree	5.9	8	1	6	15
Strychnos amazonica	Loganiaceae	Liana	5.88	7	4	1	12
Roucheria cf. schomburgkii	Linaceae	Tree	5.4	15	7	3	23
Perebea xanthochyma	Moraceae	Tree	5.32	14	4	4	7
Odontocarya tripetala	Menispermaceae	Liana	5.31	59	10	10	59
Maquira calophylla	Moraceae	Tree	4.96	8	6	4	19
Guatteria decurrens	Annonaceae	Tree	4.95	10	5	1	7
Pouteria cuspidata	Sapotaceae	Tree	4.94	5	3	5	34
Dicranostyles holostyla	Convolvulaceae	Liana	4.8	11	5	0	0

Species	Family	Life form	Biomass (gr)	Number of seeds	Number of feces	Number of visits	Number of minutes
Hieronyma alchorneoides	Phyllanthaceae	Tree	4.1	502	28	5	65
Moutabea aculeata	Polygalaceae	Liana	4	4	4	4	21
Protium ferrugineum	Burseraceae	Tree	3.8	7	2	5	97
Pouteria reticulata	Sapotaceae	Tree	3.3	3	3	1	4
Iryanthera crassifolia	Myristicaceae	Tree	3	3	2	3	7
Buchenavia parvifolia	Combretaceae	Tree	2.9	4	3	3	33
Pourouma guianensis	Urticaceae	Tree	2.75	11	6	3	8
Neea robusta	Nyctaginaceae	Tree	2.7	14	5	2	35
Paullinia cf. capreolata	Sapindaceae	Liana	2.6	6	4	2	12
Mendoncia pedunculata	Acanthaceae	Liana	2.5	8	7	6	15
Rubiaceae sp. 3 (I.N.V. 18)	Rubiaceae	Tree	2.4	2	1	1	1
Garcinia madruno	Clusiaceae	Tree	2.39	1	1	3	11
Hieronyma oblonga	Phyllanthaceae	Tree	2.3	13	5	2	5
Crepidospermum prancei	Burseraceae	Tree	2.2	6	4	4	36
Theobroma subincanum	Malvaceae	Tree	1.9	3	3	7	13
Manilkara sp. 1 (L. C-R 784)	Sapotaceae	Tree	1.82	2	2	2	29
Inga marginata	Fabaceae	Tree	1.8	6	3	4	15
Mendoncia glomerata	Acanthaceae	Liana	1.742	26	15	0	0
Phyllanthus attenuatus	Phyllanthaceae	Tree	1.738	316	41	4	72
Pouteria aff. guianensis	Sapotaceae	Tree	1.6	1	1	1	8
Buchenavia amazonia	Combretaceae	Tree	1.42	10	5	2	16
Protium cf. opacum	Burseraceae	Tree	1.4	2	2	3	21
Heisteria duckei	Olacaceae	Tree	1.23	3	3	0	0
Peritassa laevigata	Celastraceae	Liana	1.22	2	1	4	12
Souroubea bicolor	Marcgraviaceae	Hemi-epiphyte	1.1	284	59	18	69
Virola sebifera	Myristicaceae	Tree	0.96	6	4	0	0
Pouteria rostrata	Sapotaceae	Tree	0.7	2	1	2	24

Species	Family	Life form	Biomass (gr)	Number of seeds	Number of feces	Number of visits	Number of minutes
Pacouria guianensis	Apocynaceae	Liana	0.68	1	1	37	327
Calyptranthes aff. multiflora	Myrtaceae	Tree	0.65	5	5	2	15
Guatteria sp. 1 (M.G. 81)	Annonaceae	Tree	0.65	1	1	1	3
Tontelea attenuata	Celastraceae	Liana	0.65	1	1	0	0
Naucleopsis ulei	Moraceae	Tree	0.62	2	2	4	17
Theobroma obovatum	Malvaceae	Tree	0.5	1	1	3	6
Undetermined (M.G. 47)			0.45	7	5	6	23
Passiflora involucrata	Passifloraceae	Liana	0.4	7	3	1	17
Lacmellea ramosissima	Apocynaceae	Tree	0.38	4	3	2	15
Guarea glabra	Meliaceae	Tree	0.35	1	1	0	0
Fabaceae (I.N.V. 8)	Fabaceae		0.31	1	1	2	23
Inga thibaudiana	Fabaceae	Tree	0.3	1	1	1	3
Vismia macrophylla	Hypericaceae	Tree	0,2	19	3	6	62
Solanum cf. barbeyanum	Solanaceae	Liana	0,01	3	1	2	6
Undetermined species			852	2,749	711		

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Chapter 10
Ranging Behaviour, Daily Path Lengths, Diet and Habitat Use of Yellow-Tailed Woolly Monkeys (*Lagothrix flavicauda*) at La Esperanza, Peru

Sam Shanee

Abstract The yellow-tailed woolly monkey (*Lagothrix flavicauda*) is Critically Endangered and endemic to a small area of the Andean forest in northern Peru. I collected data on the home ranges, daily path lengths, diet and habitat use of two groups of *L. flavicauda*. Group follows took place at La Esperanza, Amazonas department, for 15 months between October 2009 and February 2011. The study site comprised a matrix of disturbed primary and regenerating secondary cloud forest. Home ranges were between 95 and 147 ha using 95 % minimum convex polygons, and home range overlap between the two groups was 1.6 ha. The range used by both groups varied between the wet and dry seasons. Daily path lengths were between 1.03 and 1.2 km. Fruit was the most commonly consumed dietary item followed by leaves and insects; a total of 16 plant resources were identified. There was a significant increase in consumption of leaves and insects during the dry seasons. Both groups used a variety of habitats but were only occasionally observed to use areas of white-sand forest. Home range and daily path length estimates are similar to results from studies of other woolly monkeys (*Lagothrix* spp.), although home ranges were among the smallest recorded for woolly monkeys. *L. flavicauda* at La Esperanza are less frugivorous than *Lagothrix* spp., and the estimates here are lower than those from the previous preliminary work at this site. My results suggest that *L. flavicauda* are able to survive in disturbed habitat with small home ranges and at high group densities. More research is urgently needed at other sites with different ecological conditions to enable proper conservation planning and actions.

Keywords Ecology *Lagothrix flavicauda* · Ecology yellow-tailed woolly monkey · Minimum convex polygon · Home pange overlap · Conservation

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S. Shanee (✉)
Neotropical Primate Conservation, 23 Portland Road, Stretford,
Manchester M32 0PH, UK
e-mail: samshanee@gmail.com

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10.1 Introduction

The Peruvian yellow-tailed woolly monkey (*Lagothrix flavicauda*) is one of the rarest and least studied of all primate taxa. This species is endemic to a small area of pre-montane and montane Andean cloud forest in the Peruvian departments of Amazonas and San Martin (Shanee 2011) as well as border areas of the neighbouring departments of Huánuco, La Libertad and Loreto (Shanee 2011; Graves and O'Neil 1980; Parker and Barkley 1981; Mittermeier et al. 1975). *L. flavicauda* habitat is characterized by rugged terrain of steep mountains, high ridges and deep river valleys (Shanee 2011). This area of Peru is also the centre of many sociopolitical problems caused by drug trafficking and terrorism (Shanee 2011; Young 1996; Shanee and Shanee this volume). Because of these difficulties, few previous field studies exist on this species.

Thought extinct until the mid-1970s (Mittermeier et al. 1975), *L. flavicauda* was 'rediscovered' in the department of Amazonas (Mittermeier et al. 1975; Macedo-Ruiz and Mittermeier 1979); following this, more localities and basic ecological data were published (Graves and O'Neil 1980; Parker and Barkley 1981; Leo Luna 1980; Butchart et al. 1995) along with many conservation recommendations (DeLuycker 2007; Leo Luna 1980; Rios and Ponce del Prado 1983; Shanee et al. 2008; Shanee et al. 2007). Leo-Luna (1980, 1984, 1987, 1989) carried out the first field studies on this species collecting valuable data on the species distribution, conservation, habitat preferences and diet.

Listed as Critically Endangered (CR; IUCN category A4c), *L. flavicauda* has been considered one of the 25 most endangered primate species by the International Primatological Society three times (Mittermeier et al. 2012). This species is also considered endangered under Peruvian law (Decreto Supremo 34-2004-AG) and listed in appendix I of Convention on International Trade in Endangered Species (CITES 2005). There is currently discussion as to this species' taxonomic status (*Oreonax* vs. *Lagothrix*, see Matthews and Rosenberger 2008).

Similar to common woolly monkey species (Genus = *Lagothrix*), *L. flavicauda* are large-bodied diurnal primates that live in large multi-male, multi-female groups of up to 23 individuals (Shanee and Shanee 2011a, DeLuycker 2007). *L. flavicauda* is restricted to high elevation forests between 1,500 and 2,700 m.a.s.l. and is not found in lowland Amazonian rain forests (Shanee 2011), which is rare for woolly monkeys (but see Cifuentes et al. this volume).

Habitat at high elevations is generally characterized by lower primary production levels (Lawes 1992; Smith and Killeen 1998; Costa 2006; Bendix et al. 2008; Shanee and Peck 2008). Lowered production is a function of decreased temperature, changes in soil pH and precipitation levels, thin soils and increased exposure to solar radiation and wind (Marshall et al. 2005). Conversely, primary production levels in secondary and disturbed forests can be higher than those of the primary forests (Brown and Lugo 1990). High elevation forests, even near the Equator, are also subject to stronger seasonal fluctuations in temperatures and rainfall than lowland forests. However, some sub-Andean forests have comparable fruit production levels as lowland forests (Cifuentes et al. this volume). Species found at high elevations often show ecological adaptations to better cope with the harsher conditions. These may include changes in diet, home ranges as well as daily path lengths and seasonal ranges, group sizes and habitat use (Durham 1975; Caldecott 1980; Marshall et al. 2005; Shanee 2009). The constraints of high elevation habitats are especially important for large-bodied frugivorous primates such as woolly monkeys. The ecology of common woolly monkeys is highly variable depending on forest type and primary production levels (Di Fiore and Campbell 2010; Defler 1987; Di Fiore 2003; Stevenson 2001, 2006; Defler and Defler 1996; Stevenson and Castellanos 2000).

Home ranges are defined as the area traversed by an animal or a group during its normal activities, but occasional sallies outside the area should not be included (Burt 1943). Daily path lengths can be defined as the distance travelled by an animal or a group of animals during their active period in a 24-h cycle. Both home ranges and daily path lengths are highly dependent on habitat quality, diet, resource availability and temporal fluctuations in resource availability, particularly in seasonal environments (Milton and May 1976). Body size, group size and defensibility also play roles in determining home range sizes and daily path lengths (Milton and May 1976; Mitani and Rodman 1979; Chapman 1988; Janson and Goldsmith 1995).

There exist many previous studies on the ranging behaviour and habitat use of common woolly monkeys (Di Fiore and Campbell 2010). However, no studies as yet exist on *L. flavicauda* ranging and only basic data are available on this species' habitat use and preferences (Clark 2009, Shanee and Shanee 2011a, Leo Luna 1980, 1984; Butchart et al. 1995).

I collected data on habituated groups of *L. flavicauda* at La Esperanza, Amazonas, Peru. This site has been the focus of several studies on this and other primate species (Shanee and Shanee 2009, 2011a, b). I collected data on ranging behaviour using a geographic positioning system (GPS) during group follows, as well as data on dietary preferences, habitat types and habitat use by the monkeys. This investigation forms a part of a larger conservation initiative for the yellow-tailed woolly monkey, its habitat and sympatric species (Shanee and Shanee 2009).

10.2 Methods

10.2.1 Study Site

La Esperanza is located in the *Comunidad Campesina de Yambrasbamba* on the eastern slopes of the Andes in northeastern Peru. Two permanent camps were used (Fig. 10.1) in areas known locally as *Peroles* (S 5°40′9.04″, W 77°54′14.44″) and *El Toro* (S 5°39′11.60″, W 77°54′55.79″). The study site encompasses approximately 700 ha of disturbed primary forest and regenerating secondary forest interspersed with pasture. The study site is bounded to the south, east and west by fragmented forests, pasture and agricultural lands. To the north, contiguous forest reaches to

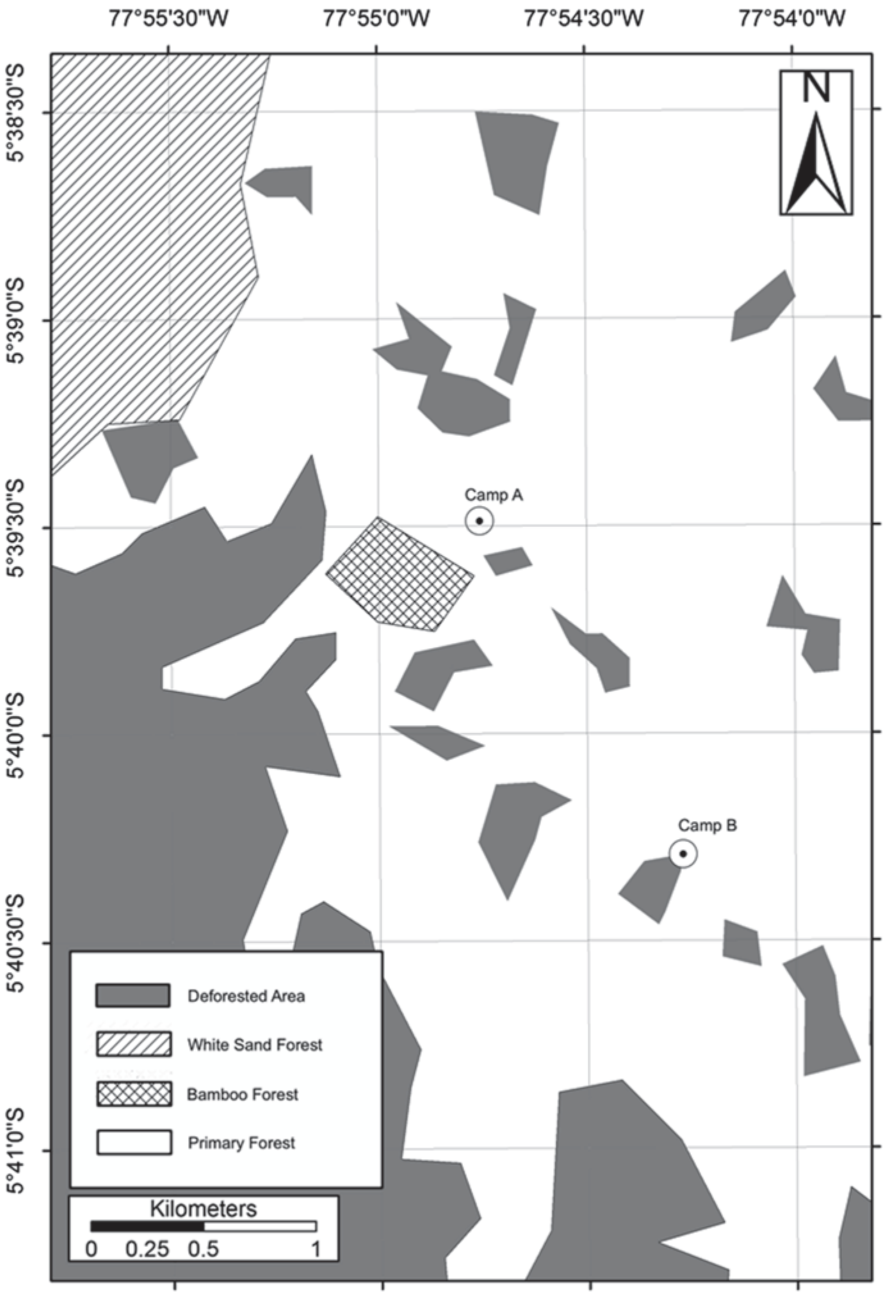

Fig. 10.1 Habitat type

the Río Maranon (approximately 100 km). This site lies in a natural forest corridor between five protected areas where the species' presence has been recorded: *Zona Reservada Rio Nieva, Santuario Nacional Cordillera Colan, Bosque de Proteccion Alto Mayo, Area de Conservacion Privada Abra Patricia-Alta Nieva* and the *Area de Conservacion Privada Pamapa del Burro* (Fig. 10.1). *Peroles* is located about 4 km north of the village of La Esperanza; *El Toro* is a further 2 km north. Both areas cover an altitudinal range of between 1,800 and 2,600 m.a.s.l. Average monthly rainfall is approximately 1,500 mm, with a dry season from August to December. Average temperature for the area is 14 °C (± 5.7). Humidity is high year-round.

The terrain is very rugged with high ridges and deep valleys. Habitat in the area is characterized by *Ficus* spp.-dominated primary pre-montane and montane cloud forest, with a thick mid-storey and understorey (Daoudi 2011; Clark 2009). The area has seen low intensity logging over the past 30 years which has removed many mature timber species.

Study Groups Data were collected on three groups of *L. flavicauda* at the two camps, resulting in 281 h of group follows. Average group size in the area was 10.7 individuals (range 3–19), including all full counts. Because of an uneven distribution of data across the three groups, I only calculated home ranges and seasonal ranges for the two groups (group A and group B) that presented the most data. Group A consisted of 15 individuals (three adult male; three adult female; six sub-adult/juvenile and three infants) and group B of 12 individuals (two adult male; five adult female; one sub-adult/juvenile and two infants).

10.2.2 Data Collection

Ranging and Path Lengths

I collected data for 15 months between October 2009 and June 2010 and between August 2010 and February 2011. Prior to this study, the area had been used for investigation on *L. flavicauda,* the sympatric Peruvian night monkey (*Aotus miconax*) and habitat characterization (Shanee and Shanee 2011a, b; Clark 2009). Therefore, clearance of new trails and other potentially disturbing preparatory work was kept to a minimum. The two study areas had been heavily logged and hunted during the 1980s and 1990s. However, these practices were not recorded during this study and were much reduced during the previous work (Shanee and Shanee 2011a, b), and primate populations in the area had previously recovered. No systematic habituation process was used on any of the study groups, as preparatory investigation suggested this was unnecessary because of the focal groups' familiarity with human presence (Shanee and Shanee 2011b). Bimonthly 5-day field trips were made throughout the study period. Data on ranging were collected during group follows using handheld GPS units (Garmin Etrex and Garmin GPSMap 60CSx). Fieldwork began at sunrise (approximately 0630 h) and continued until just after sunset (approximately 1900 h). Group follows were conducted by teams of two to three observers including a local field guide. When groups were encountered, their location was recorded as a GPS point. During group follows, I recorded additional GPS points whenever the group stopped at a new location (i.e. they were no longer moving as a group in a single direction). GPS points were recorded at the approximate centre of the group. Whenever possible, we tracked groups to a sleeping site at sunset and began the subsequent days' follow from the sleeping site prior to their waking.

Diet and Habitat Use

During group follows, I recorded data on food sources used by individuals. I recorded the type of food consumed by focal individuals for the duration of feeding bouts, recording food type every 2 min. Food types were divided into the following categories: fruit, leaf, flower, bud, insect and moss. When possible field identification was made of the plant species consumed; alternatively, when field identification was not possible, samples were taken and stored in a field press to be identified later. Identification of plants was made using previously established keys. When identification was not possible, I took samples to local botanists from the *Universidad Nacional Toribio Rodriguez de Mendoza* and the *Servicio Nacional de Areas Naturales Protegidas*. Plant samples were also deposited at the Herbarium of the *Universidad Nacional Mayor de San Marcos* in Lima.

I made a habitat map (Fig. 10.2) of the study area using data from previous work in the area (Clark 2009, unpublished data) and information from the *Zoneficacion Ecologica Economica* of Amazonas department (IIAP 2008). These maps defined areas of forest based on elevation, soil, dominant vegetation type and topographical features such as valley, slope and ridge top. I recorded the elevation in metres above sea level of the approximate centre of the group every time I took a GPS point.

Data Analysis

Ranging and Path Lengths I entered GPS point data into a geographic information system (arcGIS 9.3, ESRI 2008) and analysed it using the Home Range Tools extension (Version 1.1, Rodgers and Kie 2011). I separated points into focal groups and by season prior to estimating home range sizes, seasonal ranges and daily path length. I used two common methods to estimate home and seasonal ranges: percentage minimum convex polygons (MCPs; Michener 1979) and kernel density estimation (KDE; Worton 1989). I fit various models to find the most appropriate for the data. Before I began the Analysis, I cheked the data for duplicate points. I calculated MCPs using the fixed mean method selecting 90, 95 and 99 % of points.

For KDE, I checked the grouped points for autocorrelation and calculated the bandwidth (*h*). Using different models and proportions of the reference bandwidth, I calculated home ranges and seasonal ranges at 90 and 95 %. When range estimates from MCPs or KDE overlapped with deforested areas, I clipped the resulting maps

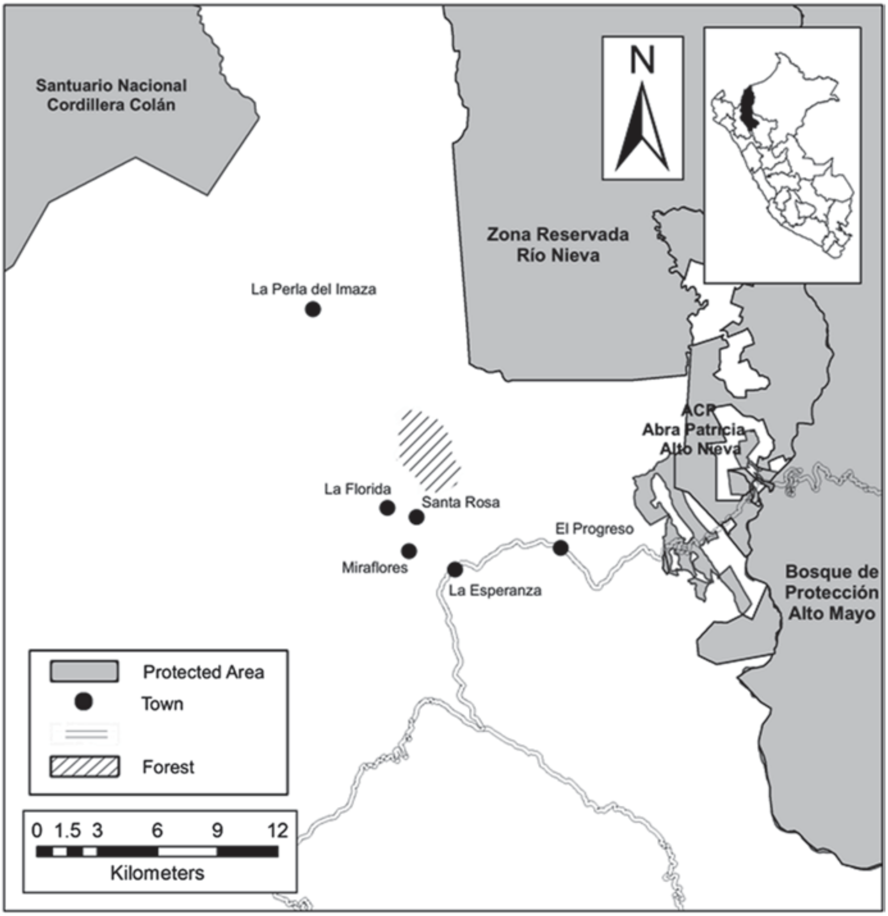

Fig. 10.2 Map of study site showing outlying protected areas and villages

to exclude these areas (Grueter et al. 2009). I also calculated territorial overlap between the groups for both home and seasonal ranges.

I calculated daily path lengths by converting point data to polylines in arcGIS using the X-Tools Pro extension (Version 8.1). I then measured the lengths of the polylines from full-day and half-day follows. I included distances travelled in half-day follows to increase the sample size (Fashing and Cords 2000; van Schaik et al. 1983). Half-day follows were evenly distributed between morning and afternoon follows to avoid possible bias (van Schaik et al. 1983). I calculated average daily path lengths for each group over the whole study period and seasonally.

Diet and Habitat Use I evaluated habitat use of the groups by overlaying home and seasonal range polygons on top of habitat maps to evaluate the use of the different forest types in the study area. This map was used to clip areas of unused habitat types from range estimates to improve accuracy (Grueter et al. 2009). Similarly, dietary data were collected during the same full- and half-day follows as ranging data using instantaneous sampling on focal animals every 2 min, recording the food type consumed (Shanee and Shanee 2011b). I analysed seasonal dietary preferences shown by focal animals during follows, looking for differences in consumption of food types and sources.

10.3 Results

10.3.1 Ranging

I analysed the data without rescaling for variance using adaptive kernels with a simple Gaussian (bivariate) model. Home ranges using MCPs at 95 % were 147 ha for group A and 95 ha for group B. Home range overlap between the two groups at 95 % coverage was 1.6 ha (Fig. 10.3). Seasonal ranges for the two groups were 120 ha for group A and 58 ha for group B during the dry season, and 82 ha for group A and 92 ha for group B during the wet season, giving an average home range of 121 ha and average seasonal ranges of 89 ha in the dry season and 87 ha in the wet season. No significant difference was found between home range estimates at 95 %.

Home ranges using KDE at 95 % were 236 ha for group A and 200 ha for group B, and home range overlap was 30 ha (Fig. 10.4). Seasonal home ranges at 95 % were 175 ha for group A and 164 ha for group B in the dry season, and 165 ha for group A and 163 ha for group B in the wet season. Seasonal range overlap at 95 % was 13 ha in the dry season and 22 ha in the wet season. No significant difference was observed between estimated home ranges at 95 %.

Results from MCP analysis were similar to estimates from previous density surveys and ad-lib observations (Shanee and Shanee 2011a); however, results from KDE were ~200 % larger. Complete results for both groups at 90, 95 and 99 % are given in Table 10.1.

10.3.2 Daily Path Lengths

Average daily path lengths were 1.03 km (SD 0.6) and 1.2 km (SD 0.9) for group A and B, respectively. Average seasonal daily path lengths were 1.7 km (SD 0.6) and 1.3 km (SD 0.9) in the dry season and 0.8 km (SD 0.4) and 0.6 km (SD 0.4) in the wet season, giving an average daily path length of 1.0 km (SD 0.8) and average daily path lengths of 1.4 km (SD 0.9) in the dry season and 0.8 km (SD 0.4) in the wet season.

Significant differences were found between daily path lengths in the dry and wet seasons for both groups ($\chi^2 = 16.01$, $P = 0.0001$ for group A and $\chi^2 = 12.60$,

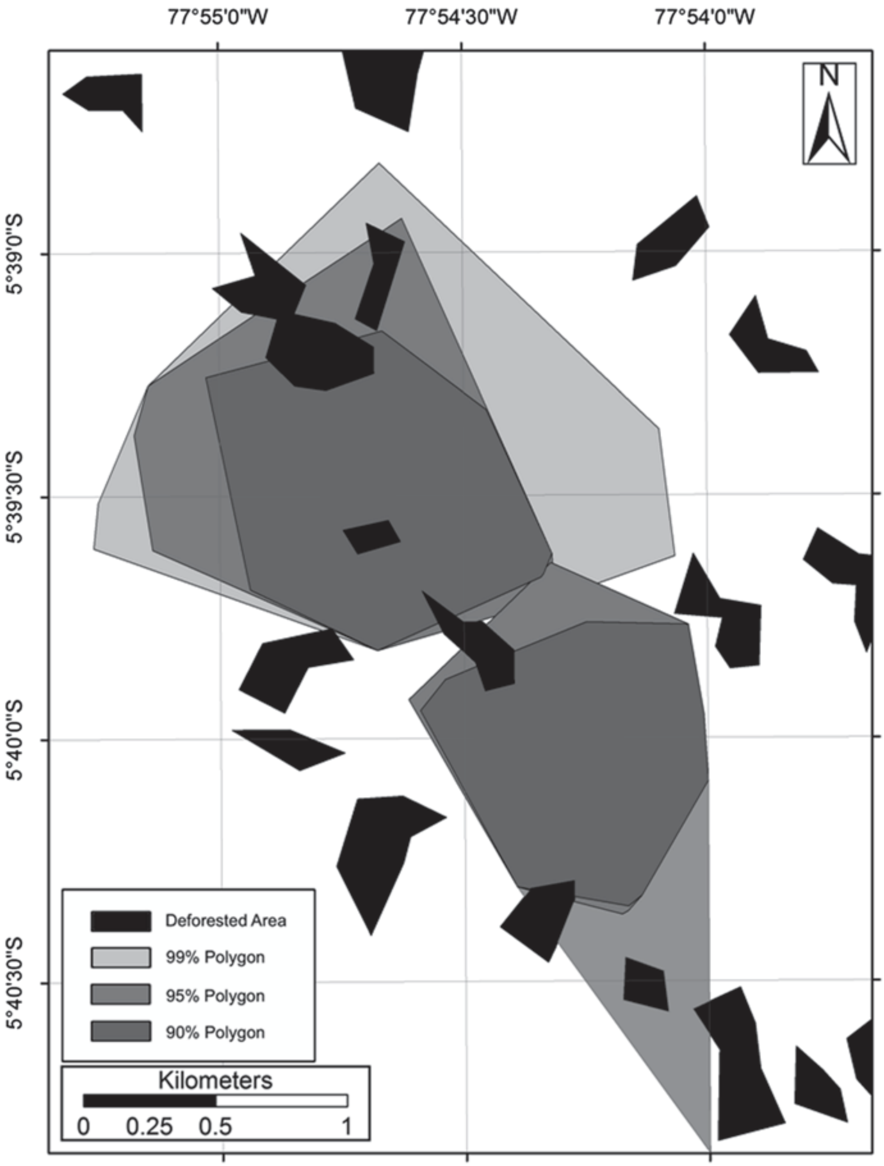

Fig. 10.3 Home range overlap between the two groups at 95 % coverage

$P = 0.0004$ for group B). Differences in average path lengths including both groups were not significant ($\chi^2 = 0.371$, $P = 0.542$).

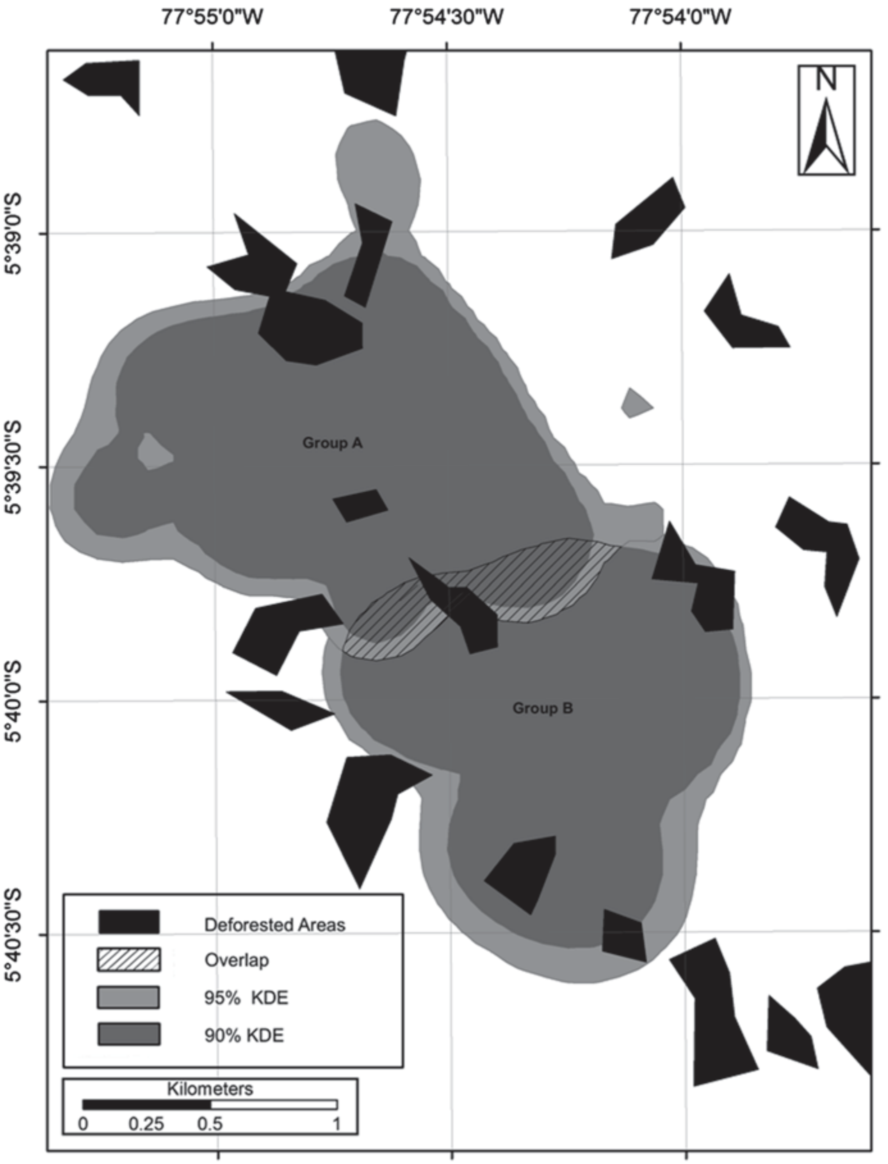

Fig. 10.4 Home range estimates using kernel density estimation (KDE)

10.3.3 Diet and Habitat Use

Diet The most common dietary item was fruit (46.3 % of recorded items) followed by leaves (23.3 %) and insects (19.1 %). Moss (6.6 %), buds (2.8 %) and flowers (1.8 %) were also consumed. I recorded a large difference in the consumption of

Table 10.1 Comparative home range and group density estimates for *L. flavicauda*

Method	Home range estimate (ha)	Group density (per km^2)	Source
Minimum convex polygons (MCPs)	91, 121, 174[a]	1.09, 0.82, 0.57[a]	This study
Kernel density estimation (KDE)	169, 218[a]	0.59, 0.45[a]	This study
Transect width estimation	96[b]	1.07	Shanee and Shanee 2011a
Krebs (1999)	107[b]	0.93	Shanee and Shanee 2011a
Ad-lib group count	86[b]	1.16	Shanee and Shanee 2011a

[a] Average estimate between both groups at 90 95 and 99 % coverage for MCPs and 90 and 95 % for KDE

[b] Calculated from density estimates given in Shanee and Shanee 2011a

Table 10.2 Plant food sources recorded for *L. flavicauda* at La Esperanza

Family	Species	Use by *L. flavicauda* (%)	Part consumed
Cercropiaceae	*C. montanta and C. utcubambana*	11.6	Fruit, leaves, buds
Euphorbiaceae	*Hyeronima andina*	0.2	Fruit, flower
Moraceae	*Ficus eximia, Ficus* spp.	67.7	Fruit, leaves, buds
Lauraceae	*Ocotea daysiflora*	1.0	Fruit
Lauraceae	*Erythrina edulis*	1.5	Fruit, leaves
Apocynaceae	–	1.4	Fruit
Bauxaceae	*Styloceras laurifolium*	2.2	Fruit, leaves, flowers
Podocarpaceae	*Podocarpus oleifolius*	0.2	Buds
Euphorbiaceae	*Croton lechleri*	0.2	Buds
Sapotaceae	*Chrysophyllum venezuelanense*	7.8	Fruit, leaves
Clusiaceae	*Clusia* sp.	1.2	Fruit
Orchidaceae	–	0.4	Flower
Sapindaceae	*Allophylus* sp.	0.6	Fruit, leaves
Bromeliaceae	–	1.3	Leaves
Additional unidentified food sources		2.7	–

fruits between the wet and dry seasons, 48.6 and 40.2 %, as well as leaves, 20.4 and 35.9 %, and insects, 20.2 and 7.2 %. There was also an increase in consumption of all non-fruit food items during the dry season. Differences in leaf consumption ($\chi^2 = 21.21$, $P = 0.0001$) and insect consumption ($\chi^2 = 31.68$, $P = 0.0001$) were found to be significant.

I identified 16 different plant food sources used by *L. flavicauda*. By far the most common food source was *Ficus* spp., followed by *Cecropia montanta, C. utcubambana, Styloceras laurifolium* and *Chrysophyllum venezuelanense* (Table 10.2). In most cases, multiple plant parts were consumed from each food source.

Habitat Use The study site consisted of a matrix of *Ficus* spp.-dominated disturbed primary cloud forest, white-sand forest, bamboo-dominated forest, ridge-top forest and deforested areas (Fig. 10.2). During follows, *L. flavicauda* did not enter areas of white-sand forest but did occasionally use this forest type during ad-lib observations; similarly, the groups only occasionally entered areas of bamboo-dominated forest and ridge-top forest, usually when passing between areas of *Ficus* spp.-dominated forest. The groups used all elevations in the study area, average 2,138 m.a.s.l. (min. 1,836 m, max. 2,429 m).

10.4 Discussion

Ninety-five percent MCPs gave the best results when compared to estimates of range sizes and group densities from transect surveys (Table 10.1). This is similar to findings from work on northern bearded sakis (*Chiropotes satanas chiropotes*; Boyle et al. 2009). Also, MCPs have been found to be more robust when sample sizes are small (Grueter et al. 2009). Home and seasonal range methods from KDE were much larger than those from MCPs and around 200 % greater than range sizes and densities from transect surveys (Table 10.1); although other studies have shown that KDEs can give accurate results (Grueter et al. 2009; Seaman and Powell 1996; Worton 1995), in this case, they seem to significantly overestimate home ranges.

MCPs can overestimate ranges with the inclusion of outlying points and if areas of un-used habitat are not removed (Grueter et al. 2009). By creating a habitat map and removing areas of unsuitable habitat, I have minimized this problem (Grueter et al. 2009); similarly, by choosing polygons at 95 % inclusion, I have reduced the effect the outlying points may have had, for example MCPs for group B at 99 % (Fig. 10.3) extended the estimated home range by ~25 % (35 ha) with the inclusion of a single point.

Home ranges of other woolly monkey species are highly variable between species and sites (Table 10.3). Unfortunately, no other home range estimates exist from other studies of *L. flavicauda,* so comparison between sites and methods is impossible. Compared to home range estimates from previous studies of other woolly monkey species, the results presented here show much smaller home range estimates than from most studies (Table 10.4) but are similar to estimates for *Lagothrix poepigii* at the Yasuni National Park, Ecuador, and *L. lagothricha* at the Tinigua National Park, Colombia, using quadrat methods and focal animal sampling, respectively (Di Fiore 2003; Stevenson 2006). The variation in *Lagothrix* spp. range sizes is possibly due to differences in group sizes, with larger groups necessitating larger areas to forage (Milton and May 1976; Dunbar 1988), although habitat quality and resource availability have also been shown to determine differences in some populations (Gonzalez and Stevenson 2009). In the case of *L. flavicauda,* reduced access to resources at elevation could necessitate reduced group sizes, as increasing home range sizes would unsustainably increase energetic demands, which may increase with elevation.

Table 10.3 Comparative home range sizes and daily path lengths for *Oreonax* and *Lagothrix*

Species	Group size	Home range size (ha)	Range overlap (%)	Average daily path length (km)	Maximum daily path length (km)	Source
Lagothrix flavicauda	15	147[a]	1.1[a]	1.03	2.49	This study
L. flavicauda	12	95[a]	1.7[a]	1.16	2.84	This study
Lagothrix cana	44–49	1,021	–	–	–	Peres 1996
L. lagothricha	13	350	65–100	–	–	Nishimura 1990
L. lagothricha	45	450	50–100	–	–	Nishimura 1990
L. lagothricha	24	760	90–100	2.88	3.58	Defler 1989, 1996
L. lagothricha	37[b]	200	–	2.0	–	Stevenson 2006
L. lugens	17–19	169	100	1.63	1.85	Stevenson et al. 1994
L. lugens	14	–	–	2.5	3.45	Stevenson and Castellanos 2000
L. lugens	17–21	–	–	1.75	2.2	Stevenson and Castellanos 2000
L. lugens	17–33	–	–	1.9	2.25	Stevenson and Castellanos 2000
L. lugens	27–32	–	–	2.45	3.2	Stevenson and Castellanos 2000
L. poeppigii	24–25	124	45	1.79	2.74	Di Fiore 2003
L. poeppigii	23	108	47	1.88	2.86	Di Fiore 2003
L. poeppigii	17–23	350	–	0.54	0.95	Soini 1986
L. poeppigii	14	400	–	–	–	Ramirez 1980
L. poeppigii	10	250	–	–	–	Ramirez 1980

[a] Values taken from 95 % MCPs

[b] Value calculated for average group size between the two study groups at the end of the study period

Again, no estimates exist for *L. flavicauda* path lengths from other studies. Daily path lengths found in this study are well within the limits of those found for other woolly monkey species, as are maximum path lengths (Table 10.3).

Table 10.4 Diet of *Lagothrix flavicauda* and *Lagothrix* spp.

Species	Fruit (%)	Leaves (%)	Flowers (%)	Buds/Other (%)	Insect Prey (%)	Source
Lagothrix flavicauda	46.3	23.3	1.8	9.4[a]	19.1	This study
L. flavicauda	71.0	–	–	–	–	Shanee and Shanee 2011a
Lagothrix cana	67.4	16.2	3.1	13.4[b]	< 1	Peres 1994[c]
L. lagothricha	78.9	11.4	0.1	4.7[b]	4.9	Defler and Defler 1996[c]
L. lugens	53	13	2	7.0[b]	25	Stevenson 2002[c]
L. lugens	60	16	1	< 1[b]	23	Stevenson et al. 1994[c]
L. lugens	78	9	–	< 1[b]	12	Stevenson 1992[c]
L. poeppigii	77	7	2	14[b]	0	Soini 1990[c]
L. poeppigii	75.5	9.8	3.5	1.9[b]	9.3	Di Fiore 1997, 2004
L. poeppigii	73	10	5	6[b]	6	Dew 2001

[a] Percent includes buds and mosses

[b] Percent 'buds' not included in study, given as 'other'

[c] Where percentages or categories were not given in the original, I have used those given by Di Fiore and Campbell (2010)

Defler (1996) found large monthly differences in areas of home range used by a group of *L. lagothricha* at Caparu, Colombia. Stevenson (2006) found a correlation between the increased use of flooded forest during the rainy season, when certain fruits are more abundant, in a group of *L. lagothricha* at Tinigua National Park, Colombia. In the same study, significant relationships were found between path length and seasonal fruit availability, habitat quality and group sizes. Daily path lengths for both groups in this study were significantly larger, and average home range increased during the dry season which coincides with reduced availability of fruits.

No study has looked at soil fertility at this or other sites with *L. flavicauda,* but the naturally lower primary production levels, a characteristic of high elevation forests (Lawes 1992; Smith and Killeen 1998; Costa 2006; Bendix et al. 2008; Shanee and Peck 2008), would suggest that this study site would be a suboptimal habitat for frugivorous primates. Habitat quality may also be low because of previous anthropogenic activities, such as logging. However, this will be at least partially offset by the higher production levels that can be found in secondary and regenerating areas (Brown and Lugo 1990). In such cases, logged forests can support high densities of Ateline primates when hunting pressure is low (Aldana et al. 2008). The densities calculated from range estimates indicate a healthy *L. flavicauda* population at La Esperanza and provide further evidence that this species is able to survive even in disturbed habitat when hunting pressure is low (Shanee and Shanee 2011a). However, more studies are needed to determine densities and ranges at undisturbed sites before conclusions can be drawn.

Leo Luna (1980) gives some details of *L. flavicauda* diets, finding that fruits are the major food source for this species and that leaves are rarely consumed, with *Ficus* spp. and *Cecropia* spp. being important food sources. Both are important food sources for *L. flavicauda* at La Esperanza. The diet of yellow-tailed woolly monkeys at La Esperanza is much less frugivorous than that of *Lagothrix* spp. (Defler and Defler 1996; Stevenson 1992; Stevenson et al. 1994; Soini 1990; Di Fiore 1997, 2004; Dew 2001) and previous preliminary estimates for *L. flavicauda* of 71 % (Table 10.4; Shanee and Shanee 2011a). Ripe fruits are replaced in the diet of this species with a higher consumption of leaves and other food items during the dry season when fruits are less available, lessening the need for larger home ranges.

Patterns of habitat use found were fairly simple, with the majority of available habitat being used year-round. The avoidance of white-sand forest will certainly be because of the lack of large fruiting trees in this forest type, which also has a much lower canopy height and thicker mid-storey and understorey (unpublished data). Although this species has been recorded in white-sand forest occasionally, it is not clear to what extent it is used. Similarly, areas of bamboo-dominated forest and ridge tops were only occasionally used, generally to gain access to other areas of forest. Stevenson (2006) found that common woolly monkeys preferred mature forests to open or degraded areas in Tinigua National Park, Colombia. Soils in white-sand forests are much more acidic (Escobedo Torres 2007), in many cases prohibiting the growth of many of *L. flavicauda's* preferred food sources. Increased exposure to wind, solar radiation, thinner soils and decreased temperatures on ridge tops also causes differences in forest structure with reduced presence of large fruiting trees. This is in addition to reduced productivity of *L. flavicauda's* preferred food source (*Ficus* spp.) with increasing elevation (Shanee and Peck 2008).

My results suggest that *L. flavicauda* is able to survive in highly disturbed habitats, with restricted ranges, allowing the species to live at comparatively high group densities. However, more research is urgently needed on this species' habitat requirements and ecology at more sites. Without data from other sites, a proper understanding of *L. flavicauda's* requirements is impossible and informed conservation actions cannot be planned or implemented.

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Chapter 11
Vocal Communication in Woolly Monkeys (*Lagothrix lagothricha lugens*) in Cueva de los Guacharos National Park, Colombia

J. Julián León, Sergio A. Vargas, Mónica A. Ramírez, Nelson F. Galvis, Edgar F. Cifuentes and Pablo R. Stevenson

Abstract Vocal communication represents several advantages for primates. Numerous studies have shown that there are different factors that affect vocal behavior. Here, we combined classic and bioacoustics methods to provide the first comprehensive analysis of the acoustic structure and the vocal behavior of a wild population of woolly monkeys (*Lagothrix lagothricha lugens*). This species is of special interest because it is one of the few neotropical primates whose vocal communication is still not understood completely. Results indicated that factors, such as the time of the day, activity, age, and sex, had major influences on the vocal behavior of the woolly monkey. We also show evidence of how call rates changed, between highland and lowland woolly monkey populations, due to intrinsic differences of each location. Acoustic structure analyses of two types of vocalizations show consistent acoustic differences among the calls of individuals in some features (i.e., call duration and high, low, and final frequency). These differences may enable woolly monkeys to distinguish between the calls of different group members. Finally, clear differences between age (juvenile vs. adult) and sex (male vs. female) classes were found, based on the structure of the alarm call.

Keywords Acoustic analyses · Contact calls · Cueva de los Guácharos · Individual recognition · Primate behavior

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J. J. León (✉) · F. Cifuentes
Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia
e-mail: jj.leon34@uniandes.edu.co

S. A. Vargas
e-mail: sergiovartro@gmail.com

M. A. Ramírez
e-mail: ma.ramirez1101@uniandes.edu.co

N. F. Galvis
e-mail: ngalvicia85@gmail.com

P. R. Stevenson
e-mail: pstevens@uniandes.edu.co

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11.1 Introduction

Vocal communication is a major component in the understanding of animal behavior, especially in social animals like primates (Snowdon et al. 1982). Primates use several signals (olfactory, visual, and acoustic) to identify other individuals and transmit information to them (Bradbury and Vehrencamp 2011). Olfactory signals transmit chemical information, which may provide clues on the reproductive status of conspecific animals and the presence of competitors, and it is generally assumed to be detectable by target individuals in a slow manner (Ceugniet and Izumi 2004). Visual contact may frequently be interrupted by several obstacles, like vegetation, especially in tropical forests (Teixidor and Byrne 1997). In contrast, acoustic signals are an advantageous way to transmit information in terms of time, space, and content (Seyfarth and Cheney 1997). These benefits make vocal communication a critical tool for diverse and important functions like social interactions (McComb and Semple 2005), cohesiveness (Struhsaker 1970; Waser 1975), predation avoidance (Neal 2009), territorial defense (Cornick and Markowitz 2002), group location (Chapman and Weary 1990), and evasion of agonistic encounters (Ramos-Fernández 2008).

Several studies of other primate species have shown that numerous factors can affect primate vocal behavior in many ways, even at the individual level, such as phylogeny (Meyer et al. 2012), home range size (Mitani and Stuht 1998), location (Wich et al. 2002), background noise (Brumm et al. 2004; Roy et al. 2011), activity (Koda et al. 2008), food (Snowdon 2009), age (Lemasson et al. 2010), sex (Hohmann 1991), cohesiveness (Mendes and Ades 2004), and the time of the day (Cornick and Markowitz 2002; Bezerra et al. 2009).

Tropical primates may benefit if their vocalizations contain information about the identity of the caller and the context in which it is emitted (Kondo and Watanabe 2009). For example, woolly monkeys in some populations show some degree of fission–fusion organization (Di Fiore and Campbell 2007), which requires information on the location of group mates and other groups. The existence and importance of individual discrimination at the acoustic level has been demonstrated in monkeys that live in fission–fusion societies, such as spider monkeys (Chapman and Weary 1990; Ramos-Fernández 2005) and chimpanzees (Marler and Hobbett 1975). Teixidor and Byrne (1999) showed evidence that spider monkeys (*Ateles geoffroyi*) can recognize other individuals for their whinnies. Furthermore, they can extract information from these calls about activity, location, and group composition of the callers. Other atelid monkey species such as the northern muriquis (*Brachyteles hypoxanthus*) has sex differences in the rates of some vocalizations (i.e., staccato and neigh: Arnedo et al. 2010).

Acoustics analyses in the family Atelidae have been studied in *Alouatta, Ateles,* and *Brachyteles* (Whitehead 1989; Mendes and Ades 2004; Spehar and Di Fiore 2013; Spehar et al. 2008; de Boer 2009; Arnedo 2010; Defler 2010). In contrast, little work has been done in this field with woolly monkeys, genus *Lagothrix*. Williams (1967), Eisenberg (1976), and Casamitjana (2002) carried out the first general descriptive studies for a captive woolly monkey population in The Monkey Sanctuary in England. In the first, a preliminary vocal repertoire was described. In the second, spectrograms were used to describe vocalizations of three captive monkeys. In the third study, a preliminary review of the vocal repertoire was made using bioacoustics methods.

Stevenson (1997) described the vocal behavior of woolly monkeys in natural conditions (Tinigua National Park, Colombia), representing the only dataset published so far. He found that the rate of calls increases by the end of the day, when individuals are more separated and when they move. In contrast, woolly monkeys emitted fewer calls in the late morning and when they were resting or feeding on arthropods. Age and sex differences were also found, because adult females emitted more vocalizations than other individuals.

In this study, we describe the vocal repertoire of a wild woolly monkey population (*Lagothrix lagothricha lugens*) at Cueva de los Guacharos National Park. We also evaluate the effect of the time of day, activity, age, and sex on the rate of contact calls. In addition, we compare the rate of calls between this highland forest and the lowland forest population studied by Stevenson (1997). Finally, we look for structural differences in the two types of vocalizations of the woolly monkey.

11.2 Methods

11.2.1 Study Site

This study was carried out in Cueva de los Guacharos National Park, located at the south of the Huila department in Colombia (01°33′N, 76°08′W) at approximately 2,000 m.a.s.l., during 6 months from January to June of 2010. The predominant habitats in the site are primary and secondary sub-Andean forests; mostly composed of open canopy forests that rarely exceed 30 m. Here, we found one of the last well-preserved Colombian cloud forest (Vásquez and Serrano 2009), where *L. lagothricha lugens* reaches a density of 21 individuals.km^{-2} (Vargas et al. 2013). The region also includes extensive zones of two types of oak forests, which are rarely used by woolly monkeys.

11.2.2 Data Collection

Vocal samples To compare our data with the vocal behavior of woolly monkeys at lowlands, we used the same methodology from Stevenson (1997) for *L. lagothricha lugens* in PNN Tinigua. We collected data on focal animals that were followed from dawn to dusk in order to complete at least 1 day of observation for adult males, one for adult females with infants, one for adult females, and one for immature individuals (juveniles and subadults). The length of focal observations was variable, and when the focal individual was lost, an individual of the same age–sex was used as a replacement within 10 min; otherwise sampling time was continued from the same time on a different day. During follows, we gathered information on the rate of calls emitted by the focal animal during a 1-min duration, and replicates were made systematically every 10 min (at 6:00 h, 6:10 h, 6:20 h, and so on). We recorded the number and type of vocalizations during that minute of observation, and we used the vocal repertoire reported by Stevenson (1997) to classify the vocalizations. During the focal samplings, we recorded the time of the day, activity of the focal individual at the beginning of the recording minute, age/sex class (adult male, adult female, adult female with young infant, and juvenile), and individual identity (when possible). The activities were categorized as movement, resting, feeding, and social activity (Gonzalez and Stevenson 2009). Within the category feeding, we considered the following diet types: fruits, leaves, arthropods, and others; the events of flower consumption were rare and included in the "leaves" category.

Calls recorded In order to identify variation between vocalizations of different individuals, we recorded different vocalizations with information on the context in which each call was emitted and caller identity, using an ad libitum sampling technique. The recordings were made at the minimum possible distance with a Sony TCM 500EV and a Tascam DR-05 recorder and a Sennheiser ME66/K6 directional microphone.

11.2.3 Data Analyses

The frequency distribution of calls did not fit a normal distribution, so we compared the rate of contact calls (number of contact calls per minute) between different daily hours, age/sex classes, and activities using Kruskal–Wallis (K–W) tests. However, we performed Tukey's honestly significant difference (HSD) post hoc tests to compare the vocalization rate between pair of categories in each variable.

Acoustic analyses were performed in RavenPro 1.4 (Bioacoustics Research Program, Cornell Lab of Ornithology). Two types of vocalizations were used in these analyses: a medium-distance contact ("normal contact") call and an alarm call ("low-frequency alarm"; Figs. 11.1a and 11.2b, respectively). Measurements were taken from spectrograms generated using a 512-point fast-Fourier transform, Hanning window function. A total of nine acoustic variables were measured for each vocalization: (1) duration (DT), (2) frequency range (FR), (3) low frequency (LF), (4) high frequency (HF), (5) maximum frequency (MF), (6) average frequency (AF), (7) entropy (EN), (8) initial frequency (IF), and (9) final frequency (FF). We selected these variables based on two considerations. First, we tried to minimize the differences between calls due to habitat degradation, animal–microphone distance, and climatic conditions. Second, these variables have been used in previous studies in *Ateles* to identify variation between individuals (Chapman and Weary 1990; Mitani et al. 1996; Teixidor and Byrne 1999).

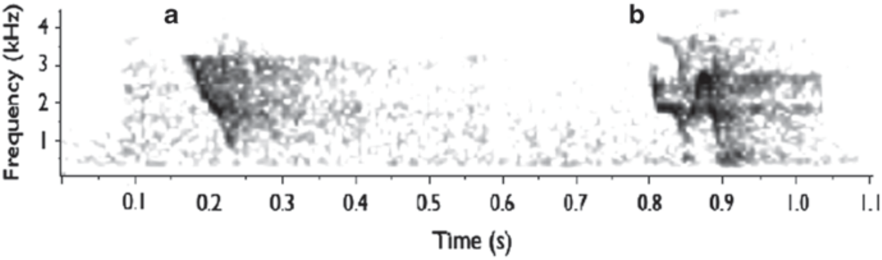

Fig. 11.1 Sonograms of two types of woolly monkey's medium-distance contact calls. **a** This type of call was used to test individual discrimination through a DFA. **b** We can see the variation of woolly monkey's contact calls; apparently, these different types of calls are used with no particular end

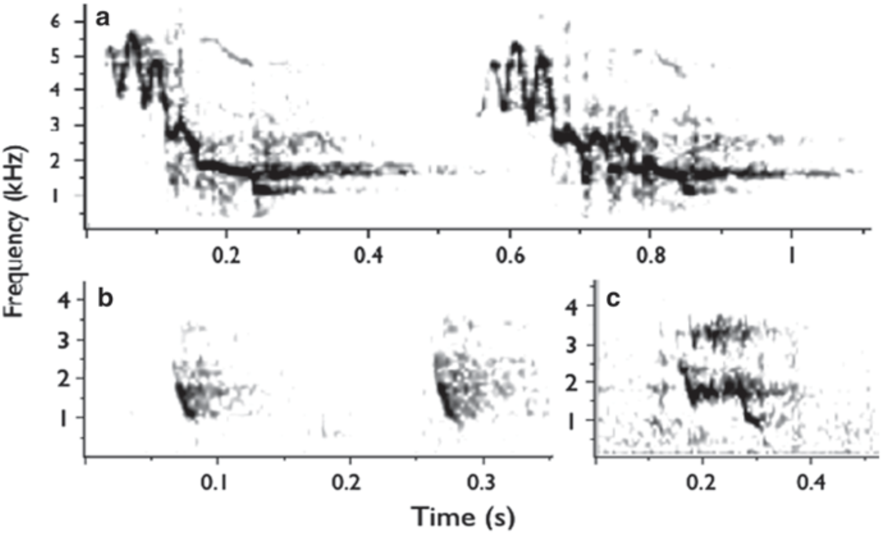

Fig. 11.2 Sonograms of four types of woolly monkey's alarm calls. **a** Alarm calls of this form were usually reordered under severe stress situations. **b** This is the most common form of the alarm calls; for this reason, we used it for testing individual discrimination through a DFA. **c** Woolly monkey's alarm calls' variations

We performed a discriminant function analysis (DFA) for each type of call. We used Pearson's correlation coefficient to examine the correlation between the acoustic variables measured in each type of call. When two variables were significantly correlated (Pearson's $r \geq 0.7$), one of them was not considered for the analyses. The medium-distance contact call's DFA was performed using a total of 44 vocalizations of six individuals and six acoustic variables (DT, LF, HF, MF, IF, FF). On the other hand, for the alarm call's DFA, we maintained six variables (DT, LF, HF, MF, EN, FF), which were analyzed for 123 vocalizations emitted by nine individuals. Statistics analyses were conducted using SPSS 15.0 and R (R Development Core Team 2008).

Table 11.1 Vocal repertoire registered for woolly monkeys at PNN Cueva de los Guacharos and frequency of each type of call during the sampling period of the focal ($n=920$)

	Specific type	Apparent sound	Frequency (%)
Contact	Medium distance	Choon	73
		Choorr	
		Cheeoor	
		Choyo	
		Cheea	
	Long distance	Chreeeoo	16.5
Alarm	Barking	Cha-Cha-Cha	4
	Mild barking	Cho-Cho-Cho	
Social interactions	Agonistic	Eca	5.6
	Grooming	Kee-Kee	–
	Play	Hooh-Hooh	0.5
		Ee-Eeoooo	
	Rejection	"Whining"	0.4

11.3 Results

11.3.1 Repertoire

In general terms, the types of vocalization and the context in which they occur in captivity and lowland forests were similar to those reported by Williams (1967) and Stevenson (1997). The vocalizations emitted by woolly monkeys can be classified into three main groups: contact, alarm, and social interactions (Table 11.1).

11.3.2 Contact Vocalizations

We can distinguish between two main types of contact calls: long-distance and medium-distance vocalizations. Long-distance vocalizations were rarely detected and mostly when individuals or subgroups were separated by a long distance from the other group members or before strong rainstorms. Medium contact vocalizations were the most common type of call (Fig. 11.1). Within this category we found several variants of similar sounds that woolly monkeys emit, but these variations do not seem to have an evident function.

11.3.3 Alarm Vocalizations

Stevenson (1997) reported two groups of alarm vocalizations associated with the type of threats, terrestrial and aerial. In our samplings, we only report alarm calls produced in response to terrestrial threats; within this type of alarm call, we can distinguish at least three forms that vary depending on the intensity in which they were emitted (Fig. 11.2). A few aerial alarm calls were heard out of the samplings, and

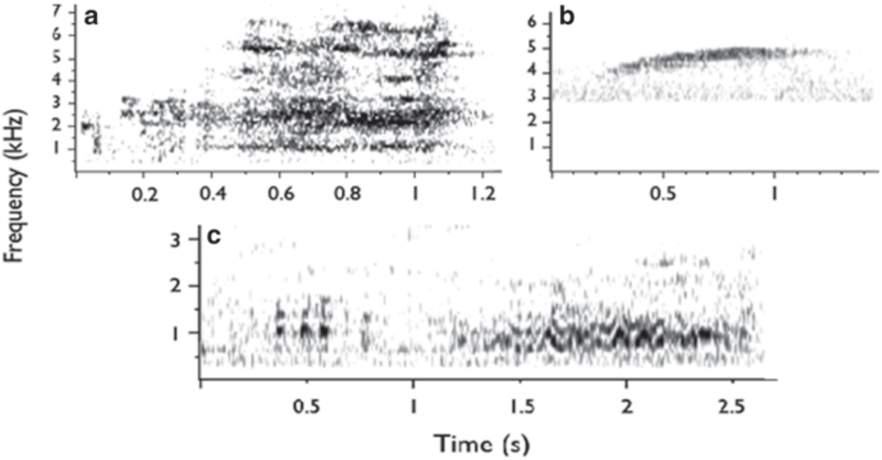

Fig. 11.3 Sonograms of woolly monkey's agonistic calls. **a** Shrieking, produced by an adult female after an aggression. **b** Whining, emitted by a juvenile male rejected by his mother. **c** Play calls emitted by two juveniles

apparently these calls were higher-frequency alarm calls and they consisted of short single units. In contrast, terrestrial alarm calls were characterized by a high number of vocalizations per unit of time, which increases with the level of threat (i.e., when the monkeys are actually looking at a predator).

11.3.4 Social Interaction Vocalizations

The most frequent social vocalizations were registered during agonistic encounters, and these vocalizations could be classified into two types of calls in this group: the shriek and the whining. The shriek is a high-frequency scream that was commonly emitted by submissive individuals who were attacked or who were involved in a rough play (Fig. 11.3a). The whining call was mostly registered in juveniles when their mothers ignored or rejected them (Fig. 11.3b). Other important calls that occurred during social interaction events were the calls produced during play activity, mostly involving juveniles (Fig. 11.3c).

11.3.5 Daytime Distribution

In order to observe the distribution of calls during the day, we grouped contact vocalizations in a 2-h period throughout the day (Fig. 11.4). We found significant differences between different daily periods (K–W test, $H=23.5$, $p<0.001$). These differences were due to the low number of vocalizations in the middle of the day, especially between 10:00 and 12:00 h, the time of the day that had a high percentage of resting (Vargas et al. 2013).

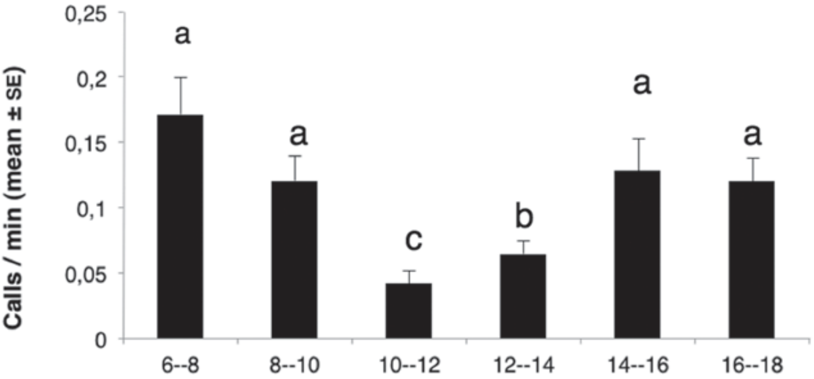

Fig. 11.4 Average number of contact vocalizations emitted by focal individuals at different times of the day. The letters above the bars indicate Tukey's test significance

Fig. 11.5 Average number of contact vocalizations emitted by focal individuals doing different activities. The letters above the bars indicate Tukey's test significance

11.3.6 Activity

The number of contact calls varied according to the activity done by the focal individual (K–W test, $H=20.01$, $p<0.01$). All the activities related to feeding events, except feeding on arthropods, had significantly more vocalizations per minute than the other activity categories (Fig. 11.5). We found that the calling rate did not vary between rest and movement. Nevertheless, when we looked at periods of 30 min, we found that the higher number of vocalizations (10) was registered when the monkeys traveled the greatest distance (426 m).

11.3.7 Age/Sex Class

The rate of calls showed significant differences between individuals of different age/sex classes (K–W test, $H=29.55$, $p<0.001$). These differences can be attributed to the

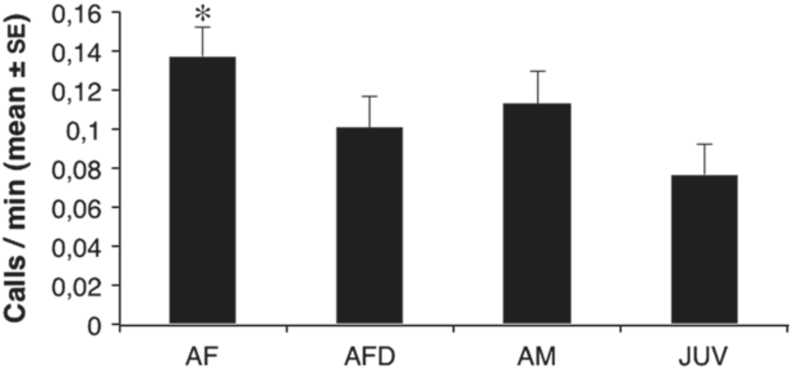

Fig. 11.6 Average number of contact vocalizations of individuals of different age/sex classes. *AF* adult female, *AFD* adult female with dependent infant, *AM* adult male, and *JUV* juvenile

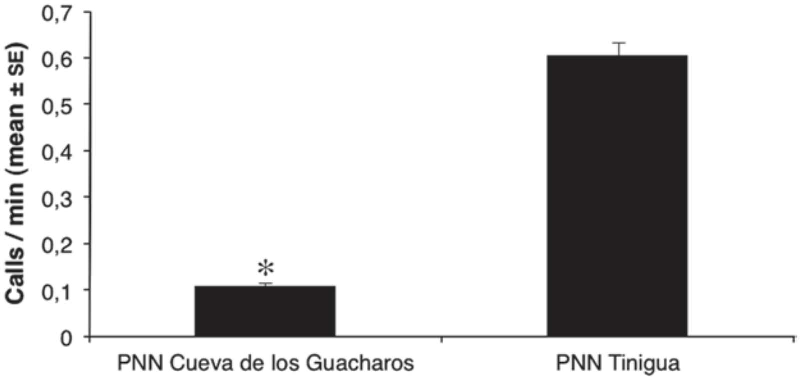

Fig. 11.7 Average number of contact vocalizations of *Lagothrix lagothricha lugens* in two different sites. *PNN Cueva de los Guacharos* represents a highland woolly monkeys' population (current study) and *PNN Tinigua* represents a lowland woolly monkeys' population (Stevenson 1997)

higher vocalization rate by adult females compared with other categories (Fig. 11.6). We did not find evidence of differences in the average number of contact vocalizations between adults, when excluding adult females, and juvenile individuals.

11.3.8 Comparison Between Sites

We compared the average number of contact vocalizations between lowland and highland woolly monkey populations, PNN Tinigua (Stevenson 1997) and PNN Cueva de los Guacharos, respectively (Fig. 11.7). We found that the rate of calls per minute was different between the two populations (Wilcoxon test, $p < 0.001$). The lowland population had a higher rate than the highland population (0.6 vs. 0.11 calls/min).

11.3.9 Individual Variation

The medium-distance contact call's DFA calculated five significant discriminant functions, with a combined $X^2 = 125.67$, df = 30, $p < 0.001$. The two first discriminant functions accounted for 83 % (57 and 26 %, respectively) of the variability among individuals. The acoustic variable that provides more information to the first discriminant function was the call duration (weight = 0.94). For the second discriminant function, we found two acoustic variables that contributed to the analysis, the high frequency and the final frequency (weight = 0.76 and 0.57, respectively). Acoustic variables with coefficient weights lower than 0.5 were not taken into consideration (Tabachnick and Fidell 1989).

We identified some individuals that were discriminated more correctly than others. For example, all the calls of three individuals were correctly assigned (AF2, SAM, and AM2). In contrast, there were individuals like the AF1 that the DFA only could assign properly 50 % of its calls. Despite there being some difficulty in finding a high degree of individual discrimination because of the variation within the individuals (Fig. 11.8), especially the AF1 and AM1 monkeys, we properly classified the majority of the calls (81.8 %).

For the alarm call's DFA, five significant discriminant functions were also calculated, $X^2 = 351.78$, df = 40, $p < 0.001$. The two first discriminant functions accounted for 86 % (62 and 24 %, respectively) of the variability among individuals for this type of vocalization. The acoustic variables that provide more information to the first discriminant function were the high and the low frequencies (weight = 0.76 and 0.53, respectively). For the second discriminant function, we found only one acoustic variable with a coefficient weight > 0.5, the duration of the call (weight = 0.81).

For the alarm vocalization, we were able to assign to the correct individual 71.5 % of the total 123 calls. As occurred with the medium-contact vocalization, we could discriminate some individuals easily than others. For example, in three individuals, ≥ 90 % of the calls were correctly assigned (Juv, SAM, and AF2). In contrast, there were individuals like JuvF, AM1, and AM2 that were correctly assigned only 53–57 % of the cases. The DFA shows age and sex differences in the acoustics properties of the alarm call (Fig. 11.9). Juveniles constantly produced alarm calls at a higher-frequency range than those produced by adult individuals, while 72 % of the calls emitted by adult females were longer than the rest of the calls from other individuals.

11.4 Discussion

11.4.1 Daytime Distribution

The decrease in the rate of vocalization of woolly monkeys in the late morning could be related to the high percentage of resting activity that occurred at this part

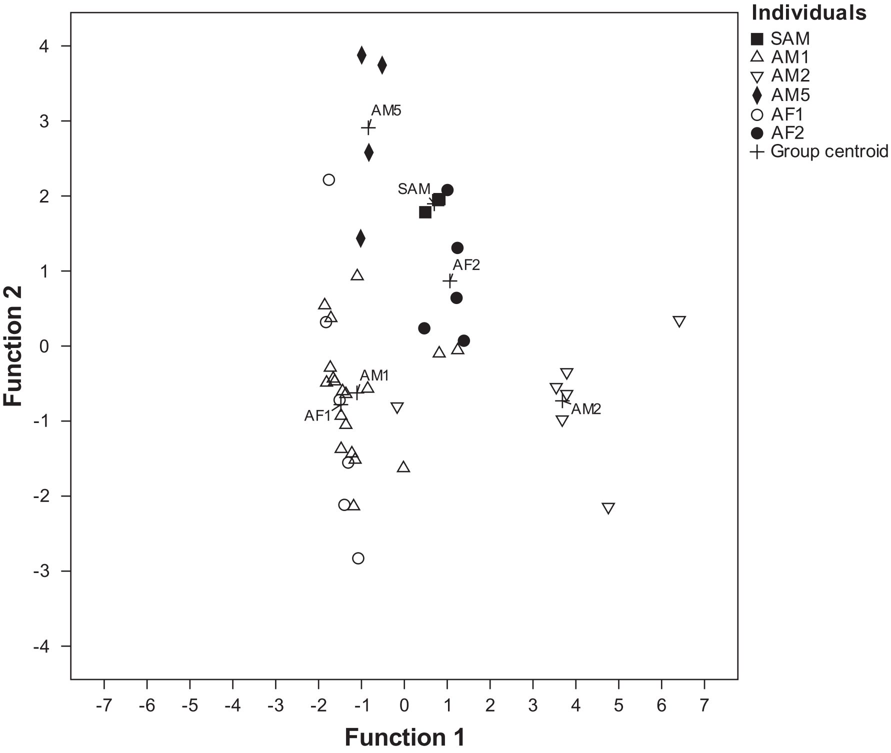

Fig. 11.8 Discriminant plot summarizing individual's differences in six acoustic parameters of the medium-distance contact call ($n=44$). The first discriminant function (Function 1; 57 %) is correlated with great values of the duration of the call ($r=0.936$), while the second (Function 2; 26 %) is mainly correlated with high ($r=0.761$), and final ($r=0.566$) frequency. *SAM* subadult male, *AM* adult male, and *AF* adult female

of the day (Vargas et al. 2013). The high frequency of contact vocalization in the first and last hours of the day can be related to the need of woolly monkeys to know the position of other group members before starting their daily activities and prior to sunset. This has been reported for other species of primates, including woolly monkeys (Mackinnon 1974; Stevenson 1997; Teixidor and Byrne 1999; Davila-Ross and Geissmann 2009).

11.4.2 Activity

We found evidence that contact vocalizations are related to feeding events, as has been suggested by other authors (Di Bitetti 2003: *Cebus*, Defler 2010: *Ateles* and *Saguinus*). Some possible explanation to this pattern could be found in the reciprocal altruism theory (Trivers 1971) which postulates that sometimes an individual can act against its own fitness in order to increase another individual's fitness, so

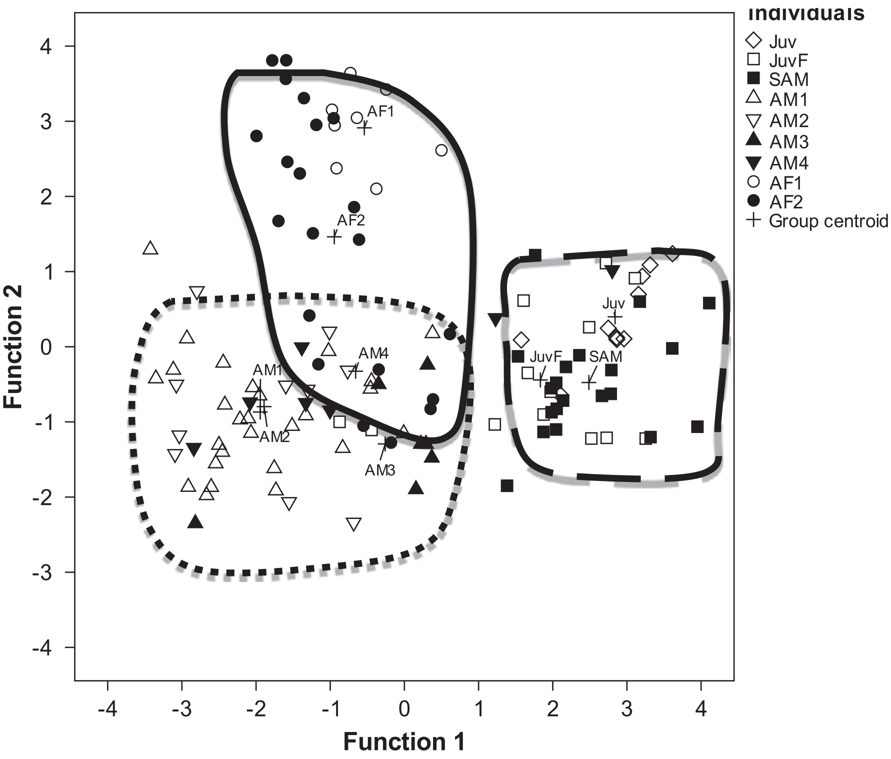

Fig. 11.9 Discriminant plot summarizing individual's differences in six acoustic parameters of the alarm call ($n=123$). The first discriminant function (Function 1; 62 %) is correlated with high values of high ($r=0.758$) and low frequency ($r=0.531$), while the second (Function 2; 24 %) is mainly correlated with the duration of the call ($r=0.812$). *Solid line* grouped 95 % of the AF's calls; *dotted line* grouped 95 % of the AM's calls, and *dashed line* grouped 95 % of the juveniles' calls. *JUV* juvenile, *JUVF* juvenile female, *SAM* subadult male, *AM* adult male, and *AF* adult female

that the other individual may act in a similar way at a later time. For example, when an individual finds a food source (e.g., fruit tree) and shares the information with other group members, we would expect that when another individual finds a food source it would act in the same way (White 1994; Stevens and Gilby 2004). Other nonexclusive explanations to the high number of calls registered during feeding events are that numerous species of primates give food-associated calls when they find or consume food to avoid aggressions (Hauser 1992), to decrease the risk of predation (Di Bitetti 2003), as a sign of comfort (Clay et al. 2012), and to increase mating opportunities and grooming (Stevens and Gilby 2004).

Although we did not find significant differences in call rates when woolly monkeys were feeding on arthropods and during other feeding activities (vegetable items), we observed a reduction in the number of calls during this activity, probably to avoid scaring potential prey when they are foraging for arthropods (Stevenson

1997). The major difference we found with the results reported by Stevenson (1997) is that our study population emitted a lower number of contact vocalization during movement than the Tinigua's population. This could be explained by differences in the degree of cohesiveness where highland woolly monkeys seem to be less cohesive than lowland populations (Stevenson et al. 1998; pers. obs.).

11.4.3 Age/Sex Class

Our results indicate that adult females emitted more vocalizations than other individuals, and this pattern has been reported for all *Atelinae* genera (Fedigan and Baxter 1984: *Ateles*, Stevenson 1997: *Lagothrix*, Arnedo et al. 2010: *Brachyteles*). This behavior could be explained by the susceptibility that adult females have to intraspecific and interspecific attacks (Stevenson 1997). In these cases, it would be advantageous for the adult females to know the location of other group members so that they can maintain an appropriate distance between them, and one way to do this is through vocal calls (Di Fiore and Fleischer 2005; Stevenson 2006; Link et al. 2009).

11.4.4 Comparison Between Sites

As shown in Fig. 11.7, there is a remarkable difference with respect to the rate of contact vocalizations between the two comparison sites. This can be explained by the low importance that cohesiveness has in the highland woolly monkeys when compared with other populations studied in different lowland places (Stevenson et al. 2002). The low degree of cohesiveness that woolly monkeys present in PNN Cueva de los Guacharos could be attributed to a low number of predators (C. Cortes pers. com.), the most likely hunters being the crested eagles and pumas. In contrast, woolly monkeys at Tinigua are exposed to five felids and several raptors, including harpy eagles (Stevenson 1996). It is also possible that woolly monkeys in the study site face low competition regimes. For instance, the density of other monkeys in the park is quite low to affect woolly monkeys (*Alouatta seniculus*: 3.9 ind.km^{-2}, *Cebus apella*: 1.4 ind.km^{-2}, and *Aotus lemurinus*; Vargas et al. 2013). However, intergroup competition is possible because the four groups we detected overlap their home ranges and the density of woolly monkeys in sub-Andean forest is relatively high (ca. 20.5 ind.km^{-2}). Woolly monkeys at PNN Tinigua show a higher density (41–50 ind.km^{-2}, Stevenson 2007) and may compete with *Ateles belzebuth* to some degree for different resources (Stevenson et al. 2000).

Arthropods constitute a large percentage of the diet of woolly monkeys in PNN Cueva de los Guacharos (39.5 %), in contrast to the PNN Tinigua population (25 %; Vargas et al. 2013). If we take into account that during arthropod feeding events vocalizations are less frequent, then we can explain some of the variations between the two sites. Considering that one of the functions of contact calls is to maintain group cohesion, to avoid predation and negative effects of interspecific competition, it is possible that the low rate found in the study area can be explained because individuals do not benefit from proximity as much as in other populations. In addition, the high frequency of arthropod feeding may also contribute to maintain low rates of vocalization (Norcross and Newman 1993; Stevenson and Castellanos 2000; Lazaro-Perea 2001).

11.4.5 Individual Variation

For the medium-distance contact call, we see, at least for one of the discriminant functions, some degree of individual discrimination for most individuals, with AF1 and AM1 being exceptions (Fig. 11.8). Similar results have been reported for other primate species (Waser 1975: *Lophocebus aterrimus*; Chapman and Weary 1990, Teixidor and Byrne 1999: *Ateles geoffroyi*; de la Torres and Snowdon 2002: *Cebuella pygmaea*; Mendes and Ades 2004: *Brachyteles arachnoides hypoxanthus*; Range and Fischer 2004: *Cercocebus torquatus atys*; Bergey and Patel 2008: *Prolemur simas*). Despite this differentiation, we found a high degree of overlapping between the individual's calls, caused by the high variation in acoustic parameters that most individuals have for this type of vocalization. No apparent sex discrimination was found based on this type of call.

Vocal communication becomes very important in primates that range and forage in subgroups because they constantly lose visual contact of other group members (Chapman and Weary 1990). Woolly monkeys do not typically live in fission–fusion societies, but present a grouping pattern and a social organization relatively flexible (Di Fiore and Strier 2004), where members of the same group often spread out over long distances during the day, but maintain some degree of group cohesion through frequent contact vocalizations (Di Fiore and Campbell 2007).

The type of contact call that we analyzed is one of the most commonly heard in foraging and movement contexts. Then, it would be advantageous for woolly monkeys to know the possible identity of one individual just by their call. In such a way, they can optimize encounters that result in beneficial interactions, like finding and following those individuals who have the best knowledge of resources or found food patches with low number of individuals (Reynolds and Reynolds 1965; Chapman and Lefebvre 1990). Also, by knowing the position of aggressive individuals, they can avoid potential aggressions (Chapman and Weary 1990).

On the other hand, we found strong evidence of age/sex discrimination in examining the alarm call, despite some degree of intraindividual variations (Fig. 11.9). There is a clear differentiation between the calls of adults and juveniles; the latter emitted significantly higher-frequency alarm calls. It has been reported that frequency parameters principally depend on different individual characteristics (Ey et al. 2007; Riede 2010). Fitch and Hauser (1995) and Fitch (1997) showed evidence that in primates, body size is negatively correlated with the frequency of vocalizations, so bigger individuals (as adults are compared to juveniles) emitted calls in a low-frequency spectrum. Also, maturation changes can accentuate these differences; for example, during puberty there is an increase in testosterone that accelerates the growth of the cartilage of the larynx (Hauser 1993).

In addition, we found less marked sex-related acoustic discrepancy in adult individuals, because males produced shorter vocalizations than females, and males can produce calls in lower frequencies (likely related to the mentioned inverse relation between body size and frequency of call). Another aspect to take into account is that sex-related acoustic differences are stronger in adults than in juveniles; this divergence is highlighted across time by the maturation changes of each sex (Bouchet et al. 2012).

Important differences in alarm calls among different age/sex individuals have been described for other primate species (Sproul et al. 2006: *Saguinus oedipus*; Pereira 1986: *Macaca* sp.; Bezerra et al. 2009: *Callithrix jacchus*; Bouchet et al. 2012: *Cercopithecus neglectus*). The capability of discriminating between individual's alarm calls can be advantageous if we consider that adult individuals have more experience and can recognize potential threats more easily than younger individuals (Sproul et al. 2006; Teichroeb and Sicotte 2012).

Our results suggest that some kind of individual recognition occurs in contact calls, and that there is a clear difference in alarm calls, depending on the age and sex of the individuals. These results show that woolly monkeys are primarily able to extract information about an individual just through their vocalizations. However, a rigorous test of this idea would require the use of an adequate experimental design.

11.5 Conclusion

Apparently, there are no differences in the vocal repertoire between highland and lowland woolly monkey populations, but the vocal behavior of each population varies depending on several socio-ecological traits. Contact vocalizations are considered the most important type of call, due to its multiple and common uses: contact maintenance, recruitment to food patches, and coordination of group movement (Casamitjana 2002).

We found that particular times of day (early morning and late afternoon) and food-associated events present the highest vocal rates; also, these rates tend to vary depending on the food resource type (fruit vs. arthropods). Woolly monkeys, especially females, use contact vocalizations to conserve appropriate distances from other individuals to avoid possible aggressions (Link et al. 2009). Further, our results suggest that group cohesiveness can significantly affect the call rate of woolly monkeys, so factors such as predators' occurrence, grade of competition with other groups and species, and forest productivity are important in understanding the vocal behavior of woolly monkeys.

The discriminant analyses performed on 167 calls (medium-distance contact call = 44, alarm call = 123) indicate that call duration and frequency are important acoustic parameters in order to discriminate individuals. Apparently, vocalizations with complex acoustic structure, like medium-distance contact calls, present a high variation in acoustic parameters that produce an elevated overlapping level between individuals' calls. Similar results have been reported by Chapman and Weary (1990) and Teixidor and Byrne (1999) for spider monkeys' whinny, another complex call from an atelid monkey.

On the other hand, simple vocalizations present few variations that lead to better individual discrimination. For example, alarm calls present consistent acoustic differences between calls of different age/sex individual woolly monkeys. Body size and morphological properties of age that change with the maturation of individuals can explain some of the differences that we found in age/sex classes (Hauser 1993; Mitani and Stuht 1998; Bouchet et al. 2012).

To gain better understanding of the vocal behavior of woolly monkeys, evidence is needed, indicating that (1) woolly monkeys can discriminate calls between different individuals, and (2) classify those calls depending on the context in which they were emitted. This evidence can be obtained with playback experiments.

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Chapter 12
Potential Determinants of the Abundance of Woolly Monkeys in Neotropical Forests

Pablo R. Stevenson

Abstract The most important proxy of species extinction is rarity, which is usually associated with low population abundance. Woolly monkeys are severely threatened and few studies have compared the abundance of woolly monkeys across the Neotropics. In this study, I analyze the abundance of woolly monkeys (*Lagothrix* spp.) and I postulate the most likely ecological factors determining the variation in their biomass. I compiled information from ca. 50 Neotropical sites, including estimates of fruit production, climatic parameters, plant composition, and information on primate assemblages. I used simple regression models at three scales: Neotropics, within their geographic range, and where they occur. At the largest spatial scale, several variables that are known to vary with latitude were highly associated with the abundance of woolly monkeys (e.g., rainfall, number of dry months, and plant species richness). However, their explanatory power decreased at smaller scales, suggesting strong biogeographic effects determining their distribution. Overall, I found that the most important variables explaining the abundance of woolly monkeys across scales were fruit production and the abundance of some key resources (i.e., *Inga* spp.). As fruit production seems to be associated with high soil fertility near the Andean mountains, this region should be a priority for the conservation of this species.

Keywords Atelinae · Ecological factors · Fruit production · *Lagothrix lagothricha* · Primate abundance · New-World monkeys

12.1 Introduction

The most important proxy of local species extinction is rarity, which is usually associated with low population density (Rabinowitz 1981; Mace et al. 2008). Woolly monkeys are severely threatened due to habitat destruction, hunting, and illegal trade (Stevenson and Link 2008; Defler 2010). Although, several analyses have demonstrated the effects of hunting on woolly monkeys (Peres and Palacios 2007),

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P. R. Stevenson (✉)
Departamento de Ciencias Biológicas, Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los Andes, Carrera 1 No 18a−10., Bogotá, Colombia
e-mail: pstevens@uniandes.edu.co

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the natural factors that affect their populations remain poorly studied. There are many factors known to affect the size of primate populations, including physical conditions, resources, and interspecific interactions. Among these factors, bottom-up theories suggest that the available energy in the habitat and primary productivity are the most important factors determining the structure of communities (Brown 1981; Currie 1991). Given that plants capture a fraction of the solar energy, and this energy decreases as it is transformed and used by consumers at higher trophic levels, the abundance of primary consumers will depend on plant productivity and plant resource allocation (Brown 1981). Thus, if more energy is available for production, this may result in either larger populations or more species in the environment (Stevenson 2001). The limited amount of energy available for consumers has to be partitioned in some way among all species present, depending on the competitive effects and niche partitioning.

Several comparative studies have demonstrated that a variety of factors influence primate populations, including biogeographic history, predation, competition, and resource availability. For instance, woolly monkeys are restricted to Amazonian and some Andean forests but are absent from the Guyana, Mesoamerica, and other subtropical forests (Fooden 1963). Although there is no clear explanation for the absence of woolly monkeys in these biogeographic areas, it is possible that they have not had the time to colonize and that competition with the already established primates may have played a role.

The role of predation on primate abundance has been discussed by several researchers, especially the effects of human hunting (Peres 1997a, 1999). Drastic changes in population densities and even local extinctions have occurred in areas with heavy predation pressures, such as hunting on large-bodied primates such as woolly and spider monkeys (Peres and Palacios 2007). Competition for resources among primate species has been invoked to explain the parapatric distributions of related primate species (Waser 1987), and recent analyses suggest its strong role in shaping Neotropical primate communities (Gonzalez et al. in prep). Increased food production is likely to increase the abundance of primary consumers such as woolly monkeys, which usually spend the majority of their feeding time ingesting fruits (Defler 2010; Zarate and Stevenson, this volume).

Total fruit production may not be the only measure of food abundance for some primates, especially for large ateline monkeys that increase the consumption of leaves in periods of fruit scarcity (Stevenson et al. 1994, 2000a). For instance, in Africa, Asia, and Madagascar, where the majority of primate species rely extensively on foliage, the quality of leaves (e.g., protein-to-fiber ratio) seems to be a very good predictor of primate biomass (Oates et al. 1990; Ganzhorn 1992).

The main determinants of the abundance and diversity of Neotropical primate communities include fruit production and its variation (Stevenson 2001; Hanya et al. 2011), a relationship that holds for frugivorous, but not for folivorous monkeys. Thus, it is reasonable to expect that the biomass of woolly monkeys would be best correlated with the abundance of their preferred plant food species. In some cases, it has been demonstrated that particular plant resources may be also important such as plants of the Moraceae and Arecaceae families (Milton 1980; Terborgh 1983).

The purpose of this study is to analyze the correlation between abundance of woolly monkeys and several potential variables that may affect their biomass. These factors include fruit production and climatic and floristic variables. The main difficulty of this kind of analysis is data availability, because it is difficult to find sites with adequate information on both woolly monkey densities and estimates of fruit production and floristic composition.

12.2 Methods

I collected information on population density of woolly and other monkeys from the literature, and the data on Neotropical forest fruit productivity, structure, and composition were gathered based on Stevenson (2001, 2010). I omitted some sites where the population density of woolly monkeys was known, but the density of other diurnal primates was unknown (preventing analysis of competition by spider monkeys and other monkeys). When information was available for several sites in close proximity and in similar ecological conditions, I choose just one site to avoid spatial pseudo-replication. I excluded sites with medium or high hunting pressure (Table 12.1). I estimated the metabolic biomass of woolly and other monkeys in each site, as the product between population density and the body weight to the power of 0.75 (Peres 1993). For the body weight, I used the average value between adult males and adult females (from different sources cited in Stevenson 2001). I assumed that half of the population corresponds to immature animals, whose weight is half as that of adults (Freese et al. 1982).

I gathered information on fruit production estimates, based on fruit traps and transects, also from the literature (Table 12.1). When fruit production estimates did not differentiate between fleshy endozoochorous fruits and other types of fruits, I used a correction factor (the proportion of endozoochorous trees in vegetation plots). In all cases, phenological studies covered at least a full continuous year. I extracted information of the temporal variation in fruit production (generally including all types of fruits) from the literature or by estimating the coefficient of variation from the figures. The number of fruit scarcity months was estimated as the number of months with less than 15 kg/ha of fruits. I also included some climatic factors, such as mean annual precipitation, temperature, and the number of dry months, which may affect plant productivity.

To look for the influence of vegetation composition on the biomass of woolly monkey population, I estimated the abundance of particular taxonomic and ecological groups. For these estimates, I used information from plots totaling at least 1 ha for each site (Stevenson 2001). These studies included all woody plants with diameter at breast height (DBH) equal to or greater than 10 cm. First, I estimated the basal area of all trees belonging to species that produce fleshy fruits with seeds dispersed by endozoochory (van der Pijl 1969), in terms of meter square per hectare. The fruit type for each species found in vegetation plots was assigned based on personal knowledge, published data (van Roosmalen 1985a; Croat 1978; Gentry 1993;

Table 12.1 List of the sites included in the analyses to assess the variation in abundance of woolly monkeys across Neotropical sites

Site	Ref. Primates	Ref. Fruit production	Ref. Plant composition
Altamira (Pará, Brazil)	Peres (1997b)		
Arabela River (Western Amazonia, Peru)	Kolowski and Alonso (2012)		
Baritú Park (Northern Argentina)	Brown and Zunino (1994)		Grau et al. (1999)
Barreiro Rico (Sao Paulo, Brazil)	Torres de Assupcao (1983); Milton (1984)	Morellato (1992)	
Barro Colorado Island (Canal Zone, Panamá)	Glanz (1991)	Foster (1982); Wiederand Wright (1995); Wright et al. (1999)	Hubbell et al. unpublished data
Caparú (Vaupés, Colombia)	Peres and Palacios (2007)	Vargas and Stevenson (2009)	Cano and Stevenson (2009); Umaña et al. (2012)
Capivara NP (Brazil)	Moura (2007)		
Cocha Cashu (Madre de Dios, Perú) total		Terborgh (1983)	Terborgh unpublished
Demerara Region (Northern Guyana)	Sussman and Phillipsconroy (1995)	Cooper (1982)	
El Rey (Salta, Argentina)	Brown and Zunino (1994)	Brown unpublished	Brown et al. (1985)
El Trueno (Western Amazonia, Colombia)	Zarate-Caicedo (2009)	Stevenson and Rodriguez (2008)	
Guácharos PNN, (Huila, Colombia)	Vargas et al. (2013)	Vargas et al. (2013); Prada and Stevenson in prep	Prada and Stevenson in prep
Guanacaste (Costa Rica)	Fedigan et al. (1985)	Burnham (1997)	
Guascara Island (Corrientes, Argentina)	Brown and Zunino (1994); Rumiz et al. (1986)		
Hato Masaguaral (Guarico, Venezuela)	Eisenberg (1978); Robinson (1986)	Colonnello (1991)	
Igarapé Acú (Central Amazonia, Brazil)	Peres (1988)		
La Selva Biological Station (Costa Rica)	Fedigan et al. (1985); Chapman (1988)		Burnham (1997)
Los Tuxtlas (Veracruz, Mexico)	Estrada and Coates-Estrada (1985)	Alvarez (1984); Sanchez and Alvarez-Sanchez (1995)	Bongers et al. (1988)

Table 12.1 (continued)

Site	Ref. Primates	Ref. Fruit production	Ref. Plant composition
Magdalena Valley (Colombia)	Green (1978)	Folster and de Salas (1976)	
Manaus TF (Amazonas, Brazil)	Rylands and Keuroghlian (1988)	Klinge (1968)	Prance et al. (1976)
Maraca Island (Roraima, Brazil)	Mendes-Pontes (1999)	Villela and Proctor (1999)	Milliken and Ratter (1989)
Noel Kempff Mercado NP (Cruz, Bolivia)	Wallace et al. (1998)	Wallace and Painter (2002)	
Norberto (Santander, Colombia)	Aldana et al. (2008); Link et al. (2010)		Aldana et al. (2008)
Nouragues (Central French Guyana)	Kessler (1998)	Zhang and Wang (1995); Poncy et al. (2001); Chave et al. (2010)	
Parque Iguazú (Misiones, Argentina)	Di Bitetti and Janson, pers. comm	Placci et al. (1994)	Placci and Giorgis (1993)
Quinchas Paujil (Boyacá, Colombia)	Aldana et al. (2008); Link et al. (2010)	Aldana et al. (2008)	
Raleighvalley (Central Surinam)	Van Roosmalen (1985b)	Mittermeier (1977); Mittermeier and van Roosmalen (1981)	Schulz (1960)
Riacho Pilaga (Formosa, Argentina)	Arditi and Placci (1990)		
Samuel (Rondonia, Brazil)	Lemos de Sa (1995)		Paiva Solomao and Lisboa (1988)
San Juan (Santander, Colombia)	Link et al. (2010)		
San Juan TF (Santander, Colombia)	Link et al. (2010)		
San Martin (Meta, Colombia)	Carretero, in prep.		
SautParare (Central French Guyana)	Guillotin et al. (1994)	Puig and Delobelle (1988)	Mori and Boom (1987)
Tapajos TF (Pará, Brazil)	Branch (1983)	Brando et al. (2008)	Ferreira and Prance (1998)
Tapajos Var (Pará, Brazil)	Branch (1983)		
Tayrona (Magdalena, Colombia)	Scott et al. (1976)		
Tefe Lake (Amazonas, Brazil)	Johns (1986)		Johns (1991)
Tikal NP (Peten, Guatemala)	Coelho et al. (1976)		
Tinigua PNN (Meta, Colombia)	Stevenson (2002); Stevenson unpublished data.	Stevenson unpublished data.; Stevenson et al. (2000a)	Stevenson et al. (2004)
Tiputini (Western Amazonia, Ecuador)	Derby (2008)		Pitman et al. Unpublished

Table 12.1 (continued)

Site	Ref. Primates	Ref. Fruit production	Ref. Plant composition
Tomogrande (Vichada, Colombia)	Arguello (2012)	Correa-Gómez and Stevenson (2010); Gongora (2012)	Gongora (2012)
Tomogrande Igapo (Vichada, Colombia)	Arguello and Stevenson in prep.		
Uauacu Igapo (Central Amazonia, Brazil)	Haugaasen and Peres (2005a)		Haugaasen and Peres (2005b)
Uauacu TF (Central Amazonia, Brazil)	Haugaasen and Peres (2005a)		Haugaasen and Peres (2005b)
Uauacu Varzea (Central Amazonia, Brazil)	Haugaasen and Peres (2005a)		Haugaasen and Peres (2005b)
Urucu (Central Amazonia, Brazil)	Peres (1990); Peres (1993)		
Vira Volta (Central Amazonia, Brazil)	Peres (1997b)		
Yotoco (Valle del Cauca, Colombia)	Palma et al. (2011)		Palma et al. (2011)

Stevenson et al. 2000b; Pennington et al. 2004), and from voucher specimens at several museums (MOBOT, NYBG, COL, COAH, ANDES, and FMNH). I also estimated the basal area of fig trees and palms, which have been proposed to be very important for all frugivorous primates during periods of fruit scarcity (Terborgh 1986). I also included the basal area of all trees in the genus *Inga* spp. (Fabaceae family) and the families Moraceae and Sapotaceae, which are heavily used by woolly monkeys (Stevenson et al. 1994, 2000a; Peres 1994; Gonzalez and Stevenson 2010; Zarate and Stevenson, this volume). In addition, total basal area and plant species richness (average number of species per hectare) were also estimated and included in the analyses.

I performed simple regression analyses to assess the effect of all independent variables on woolly monkey biomass, which was log transformed to increase homogeneity of variance. It was not possible to run multiple regression analysis, where the combined effect of different variables could be statistically controlled, because the number of sites with all estimates was too low.

12.3 Results

The main predictors of abundance of woolly monkeys changed among spatial scales (Table 12.2). However, fruit production and the basal area of *Inga* species were the most consistent predictors, since both variables were positively associated at all three scales and were significant at the two scales where the number of sampling

Table 12.2 Results of simple regression analyses, in which variables listed were fitted to explain the biomass of woolly monkey populations (ln transformed)

	Neotropical scale			Range scale			Presence only		
	R^2	N	p	R^2	N	p	R^2	N	p
Annual rainfall	*0.19*	*48*	*0.002*	0.12	19	0.14	0.02	13	0.63
No. of dry months	*0.27*	*48*	*0.0001*	0.06	18	0.35	0.00	13	0.89
Temperature	0.00	46	0.90	0.12	19	0.15	0.01	12	0.75
Latitude	*0.17*	*48*	*0.003*	0.12	19	0.15	0.03	13	0.60
Longitude	0.03	48	0.27	0.13	17	0.15	*0.33*	*13*	*0.04*
Altitude	0.00	48	0.71	0.11	16	0.20	0.02	13	0.61
Fruit Production	*0.22*	*21*	*0.03*	*0.43*	*10*	*0.04*[a]	*0.72*	*5*	*0.07*
Variation in fruit prod.	0.02	19	0.68	0.03	11	0.63	0.10	6	0.53
No. of scarcity months	0.22	16	0.06	0.01	7	0.87			
Plant richness (spp./ha)	*0.30*	*34*	*0.008*	0.11	14	0.25	0.35	8	0.12
Ateles biomass	0.02	48	0.37	0.02	18	0.58	0.14	13	0.21
Biomass of other spp.	0.03	47	0.22	*0.18*	*23*	*0.04*			
Total basal area (m^2/ha)	0.01	37	0.52	0.07	13	0.37	0.00	10	0.91
Endozoochoric trees/ha	*0.33*	*24*	*0.003*	0.11	9	0.38			
Endozoochoric basal area	0.05	32	0.23	0.11	9	0.39	*0.87*	*7*	*0.002*
Palms basal area	0.03	27	0.35	0.05	8	0.60	0.43	6	0.16
Moraceae basal area	0.04	27	0.33	0.47	8	0.06	0.25	6	0.32
Sapotaceae basal area	0.03	27	0.41	0.00	8	0.97	0.42	6	0.16
Figs basal area	0.01	31	0.69	*0.78*	*8*	*0.004*	0.30	6	0.26
Inga basal area	*0.41*	*27*	*0.0003*	*0.77*	*8*	*0.004*	0.47	6	0.13

The analyses were made at three different spatial scales and, for each one, the table shows the coefficient of determination (R^2), sample size (N), and the probability that the slope of the regression is different from zero (p). Bold numbers indicate significant factors at the $p<0.05$ level

[a] This analysis excluded Cocha Cashu that was treated as an outlier

points was relatively high. The density of woolly monkeys varies, even when considering only places without strong hunting effects (Table 12.3). Four of the five highest density estimates (>30 inidividuals/km^2) were found in the western portion of their distribution, close to the Andean mountains (i.e., Tinigua National Park, El Trueno station—Colombia, Tiputini research station—Ecuador, and Areabela River—Peru).

At the Neotropical scale, I found that the abundance of woolly monkeys was positively associated with annual rainfall (Fig. 12.1a), fruit production (Fig. 12.1b), plant species richness (Fig. 12.1c), and the number of endozoochorous trees and the basal area of *Inga* species (Fig. 12.1d). Among these variables, the basal area of *Inga* species, the number of endozoochorous trees, plant species richness, and fruit production showed the highest regression coefficients, varying from 0.41 to 0.22 (Table 12.2; Fig. 12.1). I also found negative associations with the number of dry months (Fig. 12.1e) and latitude (Table 12.2). The number of fruit scarcity months was also negatively associated (Fig. 12.1f), but the analysis indicated a probability close to the level of statistical significance. I found no evidence of a direct effect of competition with spider monkeys and other primates at this scale. The effects of

Table 12.3 Study sites where estimates of primate population density are known and where woolly monkeys occur

Site	Annual rainfall (mm)	No. of dry month	T (degrees)	Fruit production (kg/ha.y)	*Inga* basal area (m^2/ha)	*Lagothrix* density (ind/km^2)
Tinigua PNN (Meta, Colombia)	2,604	3	26.1	617	1.10	44.3
El Trueno (West Amazonia, Colombia)	2,803	2	25.9	637	1.95	38.0
Tiputini (West Amazonia, Ecuador)	3,200	0	26.5		1.30	31.8
Arabela River (West Amazonia, Peru)	3,072	0				30.6
Igarapé Acú (Central Amazonia, Brazil)	2,500	4	25			30.2
Altamira (Pará, Brasil)	3,679	0	27.1			26.2
Guácharos PNN (Huila, Colombia)	2,284	1	18.8	327	1.40	20.5
Urucu (Central Amazonia, Brazil)	3,256	3	25		0.30	19.3
Tefe Lake (Amazonas, Brazil)	3,000	0	26.5			17.0
Uauacu TF (Central Amazonia, Brazil)	2,665	3	26	210		11.7
Caparú (Vaupés, Colombia)	3,950	0	25.1	317	0.38	6.6
Cahuana Island (Pacaya Samiria, Peru)	3,000	1	27			5.5
Vira Volta (Central Amazonia, Brazil)	3,679	0	27.1			4.7
Uauacu Igapo (Central Amazonia, Brazil)	2,665	3	26			0.5

The table also shows some of the climatic variables analyzed, as well as the estimates of fruit production and basal area of *Inga* species

temperature, altitude, variation in fruit production, and the basal area of other type of plants (except *Inga*) were not evident at this large spatial scale.

At the medium scale, including just the sites within the geographical range of woolly monkeys, only three variables were positively associated with their abundance: fruit production (Fig. 12.2a) and the basal area of *Ficus* (Fig. 12.2b) and *Inga* species (Fig. 12.2c; Table 12.2). The basal area of plants belonging to the family Moraceae was also positively associated (Fig. 12.2d), but the statistical analysis showed a probability just close to the level of significance ($p = 0.06$). A negative significant relationship was found between woolly monkey biomass and the biomass of other primates in the community (Fig. 12.2e; Table 12.2). It is important to note that none of the climatic variables and the factors highly associated with latitudinal patterns resulted important predictors at this spatial scale.

At the small spatial scales (only places in which woolly monkeys occur), I also found a tendency to find high abundance in sites with high fruit production

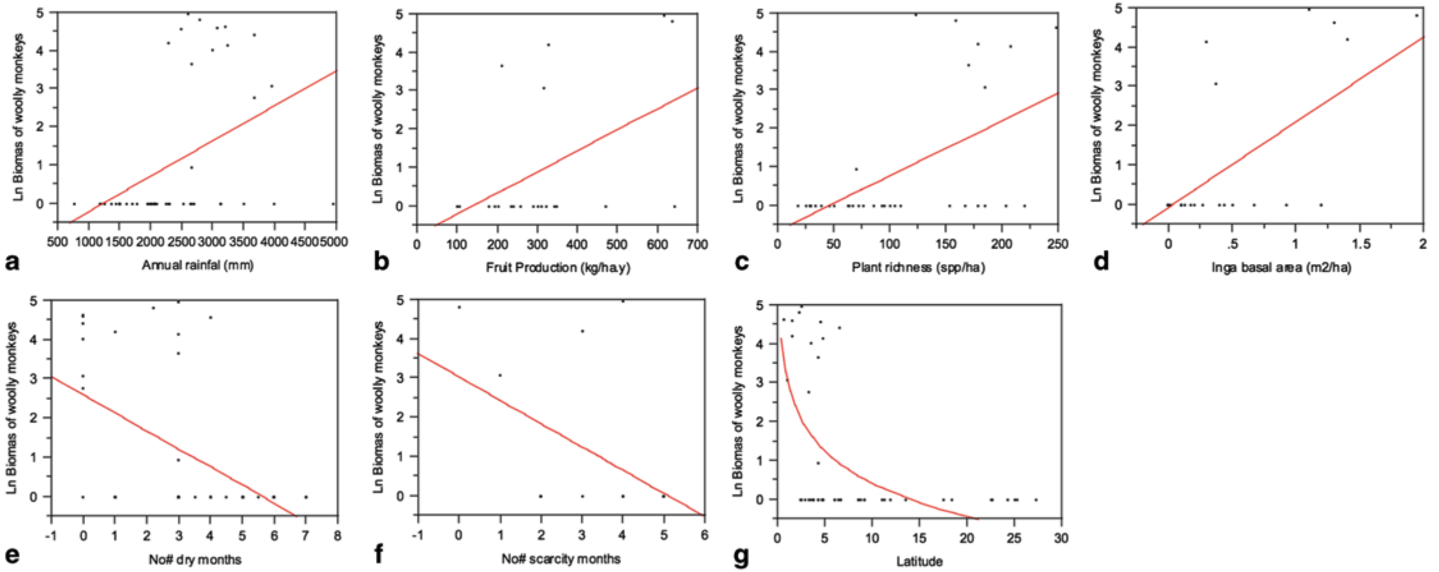

Fig. 12.1 Most important relationships between the ecological variables explaining the biomass of woolly monkeys at Neotropical sites in simple regression analyses **a** Annual rainfall, **b** Fruit production, **c** Plant species richness, **d** *Inga* basal area, **e** Number of dry months, **f** Number of scarcity months, **g** Latitude

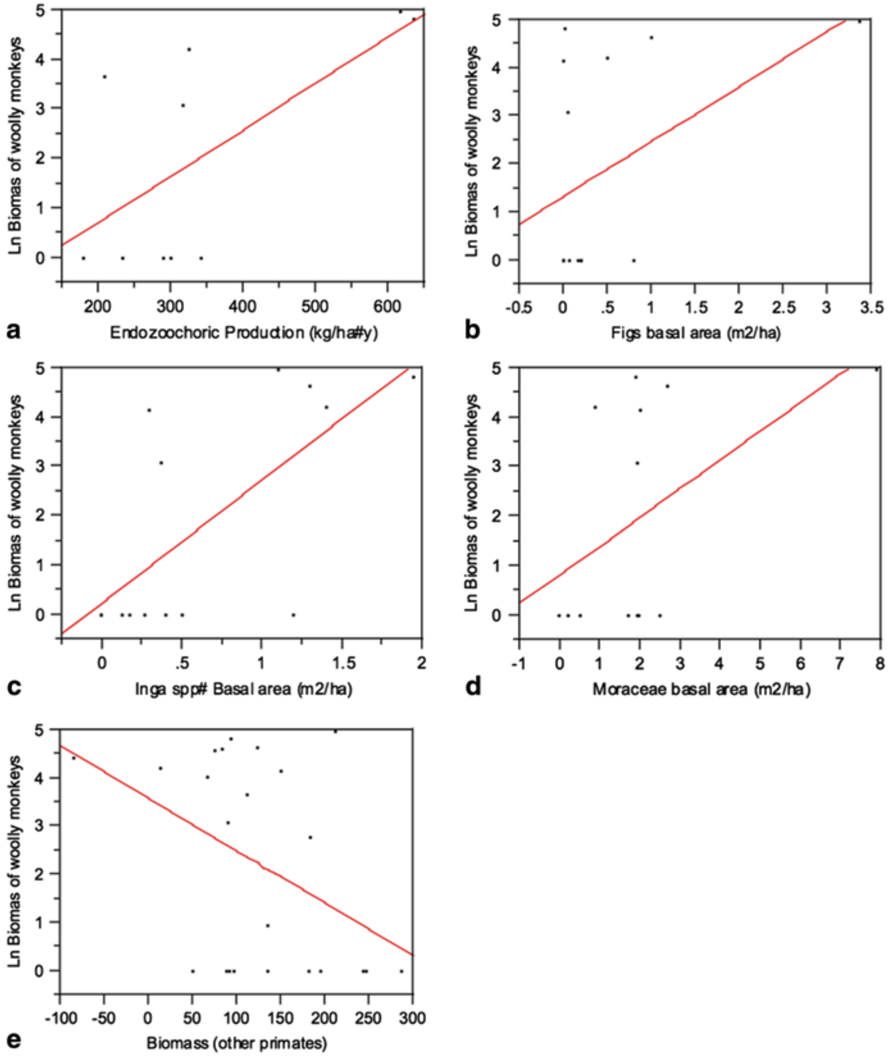

Fig. 12.2 Significant relationships between the ecological variables explaining the biomass of woolly monkeys, including just sites within their home range

and with high basal area of *Inga* species (Fig. 12.3a, b; Table 12.2). Although these variables were able to explain 72 and 47% of the variation in the abundance of woolly monkeys, perhaps for the reduced number of sites included in the analyses (6 and 5, respectively), the slope of the relationship did not result to be significantly different from zero. Instead, at this scale the only significant predictors were longitude (Fig. 12.3c) and the basal area of endozoochorous trees (Fig. 12.3d; Table 12.2).

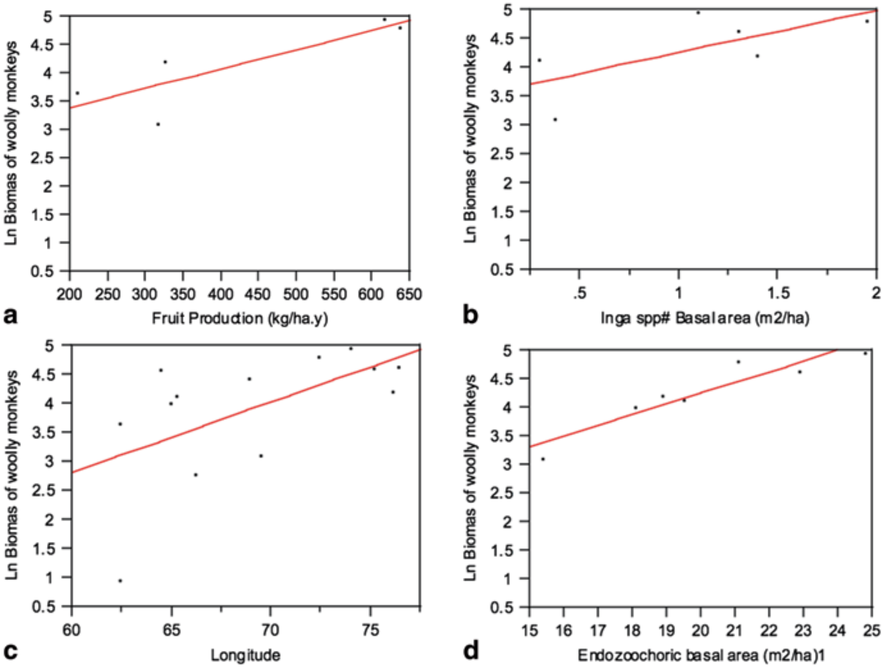

Fig. 12.3 Most important relationships between the ecological variables explaining the biomass of woolly monkeys, including places where they occur **a** Fruit production, **b** *Inga* Spp. basal area, **c** Longitude, **d** Endozoochoric basal area

12.4 Discussion

The comparative method is the main approach to determine the factors affecting the abundance of animals (Brown 1995; Symonds and Johnson 2006; Stevenson 2001). When a factor is highly correlated with the population density of an organism, it is likely that the factor is directly implicated at causing the variation in abundance or it may be just correlated with the subjacent factors driving the variation (Shipley 1999). When a large sample size is available, it is possible to use multivariate approaches to determine the partial importance of one factor, while statistically controlling the variation of other factors (Sokal and Rohlf 1995). However, the dataset compiled for this study does not have enough information on abundance of woolly monkeys and independent variables (i.e., fruit production, plant composition, and climate) for a large number of sites. For this reason, using a correlative analysis, we just can propose potential determinant variables and discuss about what factors are more likely to influence directly the density of woolly monkeys in forest with low anthropogenic influence.

At the Neotropical scale, the analyses showed high correlations between the biomass of woolly monkeys and some variables that are known to show clear latitudinal gradients. These variables included annual rainfall, the number of dry months, latitude itself, and plant species richness (Gentry 1988; Hijmans et al. 2005;

Calle et al. 2010). In addition, the production of endozoochorous fruits and the basal area of *Inga* species were positively associated with the abundance of woolly monkeys. Among these variables, the most likely causal drivers are the production of fleshy fruits and plant species richness that might increase the number of resources and decrease the chance of fruit scarcity periods (Stevenson 2001, 2005). However, the fact that recently a healthy population of woolly monkeys was described at ca. 2,000 m, where plant species richness is lower than that in lowlands (Gentry 1988, 1995), suggests that fruit production is more influential than plant diversity. This argument is supported by the fact that the association between abundance of woolly monkeys and fruit production was consistent across scales and was highly significant when sample size was not too low.

The results suggest that fleshy fruit production is the main factor explaining the abundance of woolly monkeys (as expected from bottom-up theories), and the other variables are not causing the variation in densities, but just affecting the patterns of production. It has been shown that production increases almost linearly up to 3,000 mm and then it stabilizes (Kay et al. 1997). Therefore, at large scales, including tropical and subtropical regions, the correlation between mean rainfall and abundance of woolly monkeys may just reflect that production is higher in tropical than in subtropical forests, where woolly monkeys do not occur. In addition, the number of dry months should be associated with fruit production in a mono-modal way, because very long dry periods decrease general production and too much rain decreases production by the effects of leaching soil nutrients (Clinebell et al. 1995) and increased cloud cover (Wright et al. 1999). Woolly monkeys are not present in Mesoamerica for two hypothetical reasons, because resource availability decreases in places with less than 2,000 mm of rainfall (which is common in subtropical regions) and because other primates are already using the limited resources. Interestingly, the abundance of the main competitors of woolly monkeys, spider monkeys, was not correlated with their abundance. It is likely there is a significant effect of competition, which is masked by the fact that both species required habitats with high fruit production. However, within the geographic scale, there is a negative association between the biomass of woolly monkeys and of other primate species, suggesting a relevant role of competition.

The fact that fruit production is highly correlated with the abundance of woolly monkeys is not surprising, because previous studies have determined the relevance of this variable in explaining the abundance of frugivorous primates in Neotropical forests (Kay et al. 1997; Stevenson 2001; Hanya et al. 2011). In fact, Hanya et al. (2011) found that both fruit production and their seasonality were strong predictors of primate communities in different continents. This study, in contrast, did not find a relationship between abundance of woolly monkeys and the coefficient of variation in fruit production. It is possible that monkeys are more susceptible to the length of the scarcity period than to strong variations in fruit production (in theory, a site may show large seasonal variations and still produce enough fruits even in the periods of lowest production). In fact, at the large scale, the number of months with less than 15 kg/ha of fruits showed a tendency to be negatively associated with the biomass of woolly monkeys (Table 12.2).

The basal area of some important resources for woolly monkeys was correlated across scales. The case of *Inga* species was the most consistent, and, interestingly, this genus has experienced an adaptive radiation that produced dozens of sympatric species in western Amazonia (Richardson et al. 2001), where the most abundant woolly monkey populations occur. Therefore, it is likely that coevolutionary interactions between monkeys and plants may have played a role in the patterns of migration and speciation of this genus. The basal area of palms was not a strong predictor of the abundance of woolly monkeys and this result may be explained by the fact that they do not use these resources as much as other monkeys (e.g., *Cebus apella*; Terborgh 1983). More surprising was the lack of correlation of important resources for woolly monkeys, such as plants in the families Moraceae and Sapotaceae, which are relevant dietary items in several sites (Peres 1994; Stevenson et al. 2000a; Dew 2005; Zarate and Stevenson, this volume). However, the fact that woolly monkeys are generalist consumers, ingesting fruit in proportion of its availability (Stevenson 2004), implies that their key resources may change from site to site (as it has been shown for spider monkeys; Russo et al. 2005). Therefore, it is expected that sites with a larger basal area or a large number of trees producing endozoochorous fruits would be correlated with the abundance of woolly monkeys. However, these variables were not associated at the medium scale. It is possible that in some areas the abundance of this kind of trees is not the only factor affecting fruit production, because overall this factor also depends on phenological patterns (i.e., if trees produce only at large intervals, the overall fruit production would be low in spite of a large basal area or a large number of trees).

At the smallest scale, where woolly monkeys occur, longitude was associated with the biomass of their populations. There is no reason to think on a causal relationship, but it is quite likely that this trend is associated with the fact that soils near the Andean mountains have more nutrients than soils in the central and eastern Amazonia (Quesada et al. 2010). Therefore, soil nutrients may also affect fruit and overall productivity, generating a strong effect on the population density of woolly monkeys (Defler and Defler 1996; Gonzalez and Stevenson 2010). It is possible that the correlation between the basal area of fig trees and the biomass of woolly monkeys is just a spurious effect mediated by soil fertility, and there are two reasons to suspect this idea. First, it is well known that large fig trees are more common in rich than in poor soils (Gentry 1990). Second, some of the largest trees (e.g., *Ficus insipida, F. maxima, F. boliviensis*), that are likely driving the association, produce large green syconia (e.g., Stevenson 2000; Felton et al. 2009) and are often rejected by woolly monkeys (Stevenson et al. 2000a). In contrast, woolly monkeys preferred small syconia, produced mostly by hemiepiphytic trees with low basal area (e.g., *F. guianensis, F. davidsoni, F. sphenophylla*). The presumably strong association between soil nutrients and primate abundance should be considered when prioritizing areas for the conservation of woolly monkeys, since it is clear that healthier populations can be maintained in regions close to the Andean mountains.

In conclusion, all the results and arguments show that the production of fleshy fruits is the most likely factor determining the abundance of woolly monkeys. It is likely that many factors such as mean rainfall, the number of dry months, and soil

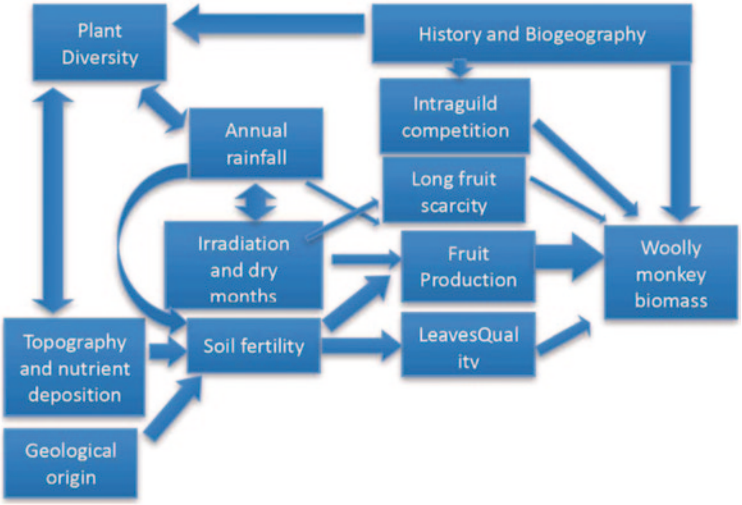

Fig. 12.4 Theoretical model explaining the abundance of woolly monkeys in Neotropical forests. The width of the arrow shows the relative importance of the causal associations

fertility are the main drivers affecting the rate of resource production for these monkeys (Fig. 12.4). I believe that this model should be tested when more information is available, making multivariate analyses possible. In addition, it is likely that the role competitors play will have an effect and that the quality of leaves will also affect woolly monkey populations. Since young leaves are the main feeding resource in periods of fruit scarcity (Stevenson et al. 1994), the quality of foliage may also affect their populations. For the purpose of understanding better the relative contribution of the factors affecting woolly monkey populations, it would be necessary to expand the number of natural sites with information of primate densities and also relevant estimates of habitat quality.

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Chapter 13

Behavioral Ecology and Interindividual Distance of Woolly Monkeys (*Lagothrix lagothricha*) in a Rainforest Fragment in Colombia

Diego A. Zárate and Pablo R. Stevenson

Abstract Woolly monkeys have been considered vulnerable to forest fragmentation. However, we found a population of woolly monkeys that has been living in a small forest remnant in Colombian Amazonia, raising questions about which factors determine the persistence or extinction of woolly monkeys in fragmented forests. The main purpose of this investigation was to describe the behavioral ecology of woolly monkeys (*Lagothrix lagothricha*) in a 136-ha forest fragment in Guaviare, Colombia. We recorded activity patterns, diet, and use of space for three monkey troops by instantaneous sampling on focal animals, and we quantified interindividual distance, between January and December 2008. This group of woolly monkeys spent on average 31.7 % of their time feeding, 32.4 % resting, 34.2 % moving, and 1.8 % in social interactions. Their main feeding items were fruits (57.2 %), followed by leaves (15.5 %), arthropods (15.8 %), seeds (5.2 %), flowers (5.1 %), and others (1.2 %). The three most used plant families for fruit consumption were Moraceae (23.4 %), Fabaceae (16.3 %), and Ulmaceae (8.3 %), and the most important species was *Ampelocera edentula* (Ulmaceae). We estimated an average daily travel distance of 2,339 m and a home range of 126 ha. We found a negative relationship between the degree of interindividual distance and group size. Most of the studied ecological parameters were within the reported ranges for woolly monkeys in undisturbed habitats. Thus, our evidence indicates that their persistence in fragments does not require drastic behavioral changes. We suggest that fragmentation represents a threat to woolly monkeys when (1) fragments are not productive enough to sustain the population and/or (2) when it leads to a higher hunting pressure on the population.

D. A. Zárate (✉) · P. R. Stevenson
Departamento de Ciencias Biológicas, Centro de Investigaciones Ecológicas La Macarena,
Universidad de Los Andes, Bogotá, Colombia

D. A. Zárate
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma
de México, México City, México
e-mail: diegozarate.c@cieco.unam.mx; diegozarate.c@gmail.com

P. R. Stevenson
e-mail: pstevens@uniandes.edu.co

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Keywords Activity patterns · Atelines · Diet · Fruit production · Group spread

13.1 Introduction

Habitat degradation usually causes changes in activity patterns, diet, home range, and group cohesion in many primate species (Muruthi et al. 1991; Tutin 1999; Marsh 2003; Irwin 2007). These changes may influence demographic parameters and many species are likely to become locally extinct in small fragments. However, some primate populations are capable of modifying their behavior as a response to habitat disturbance and fragmentation (Tutin 1999; Irwin 2007; Pozo-Montuy and Serio-Silva 2007). For example, in continuous habitats *Cercopithecus cephus* is mainly frugivorous (Chapman et al. 2002) while groups that are confined to isolated forest fragments consume fewer fruits and more insects (Tutin 1999). In *Propithecus diadema,* groups that reside in fragmented areas have less intragroup cohesion than groups that occupy continuous habitats, mainly as a response to an increase in intraspecific competition for food, given the reduction and variation in the distribution of their resources (Irwin 2007). This is a similar response to the one found in spider monkeys (*Ateles* spp.) and chimpanzees (*Pan* spp.) with less-cohesive and more flexible societies that have adopted a fission–fusion system of social organization (Symington 1990).

Other primates like howlers also show a high degree of dietary and behavioral flexibility that allows them to adjust to different degrees of habitat disturbance (Silver and Marsh 2003; Pozo-Montuy and Serio-Silva 2007). However, they tend to be more vulnerable to hunting, disease, predation, and endogamy in isolated populations (Bicca-Marques 2003). On the other hand, small primates such as *Callithrix argentata* can show a tendency towards an increase in population densities in fragments. This could be explained by the effect of density compensation, caused by an increase in resource availability when large primates are absent (Peres and Dolman 2000). However, the long-term viability of their populations may depend on genetic diversity, which is probably lower in fragments (Rodríguez-Toledo et al. 2003).

The fact that woolly monkeys (*Lagothrix* spp.) are absent from most small forest fragments suggests they are one of the most vulnerable primates for habitat disturbance and forest fragmentation (Bernstein et al. 1976; Peres 1994; Defler and Defler 1996; Di Fiore and Rodman 2001; Stevenson 2010). In addition, woolly monkeys have been described as large-bodied frugivores (Stevenson et al. 1994; Peres 1994; Defler and Defler 1996; Di Fiore 2004), a guild usually associated with a high risk of local extinction in fragments. Group size is variable (10–49 individuals; Peres 1996), and groups exhibit some degree of cohesiveness (Stevenson et al. 1994; Stevenson 1998; Dew 2005). Their low reproductive rates (Nishimura 2003) and large activity areas make it unlikely that woolly monkeys will survive in forest remnants (Milton 1993; Tutin 1999; Onderdonk and Chapman 2000; Gilbert 2003; Ferrari et al. 2003; Marsh 2003).

Although it has been suggested that large frugivorous primates are the first to become locally extinct in the smallest forest fragments (Estrada and Coates-Estrada 1996; Gilbert 2003; Michalski and Peres 2005), we found a population of woolly monkeys living in an isolated forest fragment in Colombia for more than 20 years (Stevenson, pers. obs.). Here, we aim to describe for the first time ecological and social variables of woolly monkeys living in forest fragments in order to establish differences and similarities between this population and populations in continuous forest. The specific objectives of the study were: (1) to quantify the activity patterns, diet, use of space, and cohesiveness between woolly monkey groups and their age/sex classes; (2) to quantify the fruit production and to evaluate the influence of monthly fruit production on activity budgets; and (3) to compare the activity budgets in a forest fragment with continuous forest. In addition, we discuss the factors that might have allowed this population to survive and persist in the fragment.

13.2 Methods

13.2.1 Study Area

The study was carried out in a forest fragment belonging to the experimental station El Trueno of the Instituto Amazónico de Investigaciones Científicas (SINCHI) located near El Retorno town (Departamento del Guaviare, 2° 22′ N, 72° 41′ W; Fig. 13.1a) in Colombia. The station includes a fragment of 136 ha including both flooded and terra firme rainforest. The fragment contains high plant species richness with dominance of pioneer species (mostly *Croton matourensis* and *Cecropia sciadophylla*; Stevenson and Rodríguez 2008). Other important plant species include *Iriartea deltoidea, Oenocarpus bataua, Pourouma minor,* and *Pourouma bicolor,* and the most common families are Moraceae, Fabaceae, Urticaceae, Euphorbiaceae, and Burseraceae. The site has a mean temperature and rainfall of 25.9 °C and 2,448 mm, respectively (IDEAM 1999).

Eight primate species inhabit the fragment (*Lagothrix lagothricha, Alouatta seniculus, Saimiri sciureus, Callicebus torquatus lugens, Saguinus inustus, Cebus albifrons, Sapajus apella*, and *Aotus sp*.) of which woolly monkeys are the most common, with a density of 50 individuals/km^2. This estimate is similar to what has been found in continuous forest with high densities of woolly monkeys such as Tinigua National Park (41–50 ind/km^2; Stevenson 2007) and Ecuadorian Amazonia (31 ind/km^2; Dew 2005).

13.2.2 Data Collection

We studied all three groups of woolly monkeys that lived in the forest fragment (Table 13.1). The large “L” group was followed from January to December of 2008;

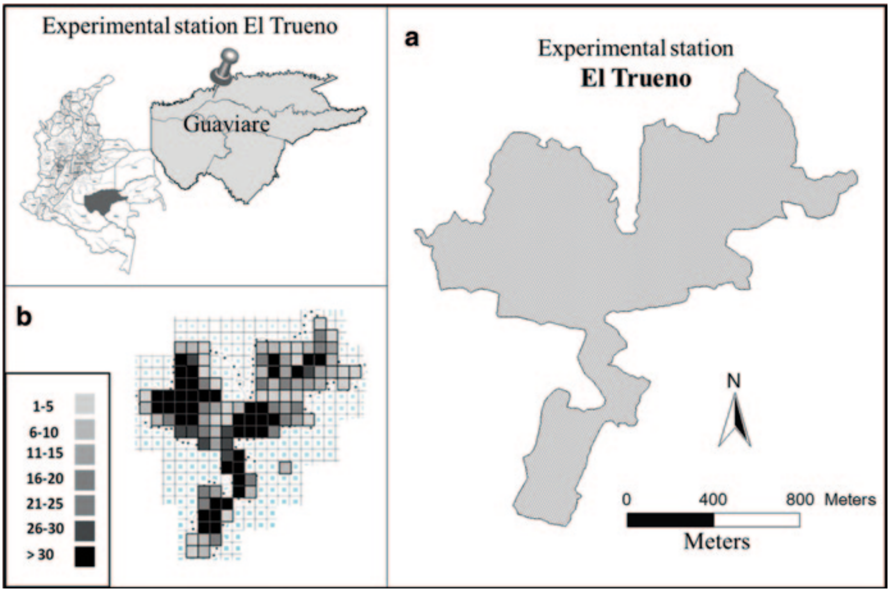

Fig. 13.1 (**a**) Map of "El Trueno" experimental station, Instituto Amazónico de Investigaciones Científicas SINCHI. (**b**) Total area used by all groups of woolly monkeys in the forest fragment (136 ha). The gray patterns represent the frequency of use for each of the 1-ha quadrants. This scale is based on instantaneous samples every 30 min, where lighter patterns represent less frequently used quadrants and darker patterns represent more frequently used quadrants

Table 13.1 Composition of woolly monkey groups present in a forest remnant in El Trueno Station, Guaviare, in Colombian Amazonia

Group	Adult male	Adult female	Subadult male	Juvenile	Infant	Newborn	Total
L	11	18	1	–	2	11	30–32
M	8–9	11–12	?	2	3	?	21–24
S	5	8	1	2	2	2	16

the medium-sized "M" group was followed from January to April; and the small "S" group was followed from May to December. The M group was impossible to monitor all year, because its home range included an area (29.4 ha) that was regularly flooded.

We followed two of the three groups during 5 days for each group, usually in consecutive days at the beginning of each month. All members of the groups were individually recognized. Genital marks, injuries, particular facial expressions, and body size were used to distinguish individuals. We collected data on activity patterns and diet (see below) using instantaneous sampling on focal individuals every 10 min (Stevenson et al. 1994), a method that has been recommended (González and Stevenson 2009). Each focal individual was followed continuously for 12 h (72 instantaneous samples) for each day of data collection, usually between 0600 and 1800 h. Thus, we recorded 360 instantaneous samples in 5 days of sampling each month, totaling 4,320 instantaneous samples for a group in 12 months (8,640 in total). Three different age/sex classes were observed in each group: two adult males, two adult females without infants and one adult female with dependent infant (< 1-year-old). All focal individuals selected were habituated and the same animals along the study, but the sequence in which they were followed each month was not established a priori.

Activity was classified as moving, resting, feeding, or social interactions (as defined by González and Stevenson 2009). Different food items were identified and classified as fruits (ripe and unripe), seeds, leaves, flowers, arthropods, and other types rarely ingested (termite nest, water, or vertebrate prey). In addition, we quantified the time each focal animal spent feeding on each of the food types (except for arthropod feeding) in a continuous fashion (Stevenson et al. 1994). The moment when we detected food ingestion was considered as the initial time, and the time at which the animal stopped consuming items for more than 1 min, or when the animal moved away from the feeding source, was considered as the ending time (Stevenson et al. 1994).

Using a global positioning system (GPS; Garmin 76 CSX map), we registered the location of the focal animal every 30 min, and we referenced these positions in a 1-ha grid (Stevenson 2006). We used these positions to estimate daily traveled distance using Mapsource version 6 (2008).

13.2.3 Interindividual Distance

To quantify the distance between individuals, we selected another five focal animals from the same groups and from the same age/sex classes as the main focal animals. These additional focal animals were simultaneously followed by a second observer, who gathered information on the position of the animal using another GPS at 30-min intervals. The selected focal animals were individually recognized and the pair chosen each month was determined randomly each month. Thus, to quantify the degree of separation between individuals, the linear distance between the main focal animals and a secondary focal animal was estimated using Mapsource version 6 (2008). In total, we measured 1,440 sample points of linear distance between simultaneously followed focal individuals in the same group during the study.

13.2.4 Fruit Production

Fruit production estimates were calculated following the methodology used by Stevenson and Link (2010), using 10 km of phenological transects. The transects were monitored twice a month during 12 months, looking for fruits or parts of them on the trail floor and estimating crop size visually (number of fruits in the plant) by counting the fruits of several tree branches and then multiplying by the number of branches in the plant. First, we estimated the average dry weight of fruits (>5 fruits) of every species in transects. We multiplied dry fruit weight by the total crop size in each individual plant sampled. Then, individual fruit production was assigned to the effective sampling area, by estimating the effective transect width, using information on the perpendicular distance from the producing trees to transect because larger plants are detected in linear transects at larger distances than smaller plants (Stevenson 2002). For this purpose, we regressed diameter at breast height (DBH) of fruiting trees on the perpendicular distance to transect and selected six of the farthest points of the distribution to estimate the effective width for each plant size (distance $=(0.028 \times \text{DBH})+5.45$ m). Finally, we calculated a community-wide estimate of fruit abundance in units of production (fruit mass.ha^{-1}.mo^{-1}), summing individual productions, which take into account the effective sampling area.

13.2.5 Data Analyses

Comparisons between pairs of groups were made only considering those months when both groups were followed (January–April, L Group vs. M Group; May–December, L Group vs. S group).

Activity patterns and Diet We calculated the proportion of instantaneous samples in each activity and diet category every day, and we used each day as a sampling unit for statistical comparisons between groups and age/sex classes. We used binomial Z tests for two proportions to assess these comparisons, except in cases of infrequent behaviors (when we used analysis of variance (ANOVA) or the Kruskal–Wallis test (in the cases with nonparametric values) and T tests). In order to compare among age/sex classes, we combined data from the 2 days following adult males and adult females without dependent offspring. We used ANOVA or the Kruskal–Wallis test (in the cases with nonparametric values) to evaluate monthly variations in activity patterns and diet, using the percentage of each sampling day as statistical units. We performed Pearson correlation analysis to determine the influence of monthly fruit production on activity budgets. All analyses were done using the Statistical Product and Service Solutions (SPSS) program (SPSS 17 2008).

Use of space To evaluate if there were differences between the daily traveled distances between groups, we used T tests each month, using daily path length of each individual followed as sampling units. Comparisons were only made between the periods when the two different group pairs were followed. We performed a one-way ANOVA for each group to evaluate whether there were monthly differences between the daily traveled distances along time. To compare home range areas, we constructed accumulation curves between the number of 1-ha quadrants used by the different woolly monkey groups, as a function of instantaneous sampling points recorded in each quadrant. For this purpose, we used the EstimateS program (Colwell 2005).

Interindividual distances To establish whether the interindividual distance distribution differed among groups, we constructed a frequency distribution curve for each group. We grouped interindividual separation distances in categories of 20 m. We evaluated differences between groups using Kolmogorov–Smirnov tests (Sokal and Rohlf 1995).

13.3 Results

13.3.1 Activity Patterns and Diet

Throughout the study year, individuals of the L group were seen resting 32.4 % of the time, 33.8 % feeding, 32.6 % moving, and 1.2 % on other activities ($n = 4{,}320$ instantaneous samples). Activity budgets for the M group were 24.4 % resting, 31.1 % feeding, 41.3 % moving, and 3.2 % on other activities ($n = 1{,}440$) and for the S group 40.3 % resting, 30.2 % feeding, 28.6 % moving, and 0.9 % on other activities ($n = 2{,}880$). We did not find significant differences in the type of activity between groups L and M (Fig. 13.2a). However, feeding was more frequent in group L than in group S ($t = 2.460$, df = 8; $P = 0.039$). We found few differences in activity budgets among age/sex classes (Fig. 13.3), and the main difference was in feeding behavior, which was more frequent for adult females with a dependent infant in the L group (adult female with a dependent infant vs. male and female adult: $Z = 2.689$, $P = 0.006$; $Z = 2.085$, $P = 0.031$). Although this tendency was evident for all three groups, we did not find a significant difference between age/sex classes and behavior for the M and S groups (Appendix 13.1a).

In general, the most frequent items in the diet were ripe fruits (57.2 %), followed by young leaves (15.5 %), arthropods (15.8 %), seeds (5.2 %), flowers (5.1 %), and others (1.2 %). We did not find significant differences in diet composition between groups (L vs. M groups and L vs. S groups). However, young leaves consumption was more frequent in the L group ($t = 2.507$, df = 8, $P = 0.036$), and the consumption of arthropods was more frequent in the M group ($t = -2.852$, df = 8, $P = 0.021$). We did not find significant differences in diet composition between the age/sex classes in the groups (Appendix 13.1b). However, in group L, the adult females with dependent infants had a tendency to consume more young leaves than other age/sex classes (Fig. 13.3).

Diet composition varied over time (Fig. 13.4). Group L showed temporal differences in the frequency of consumption of all feeding items (Appendix 13.1c), and group S showed lesser temporal differences, because they were followed for a lesser period of time. We estimated annual fruit production to be 685 kg/ha/year, and it varied throughout the year. We found that monthly fruit production was a good predictor of feeding time ($P = 0.005$, $N = 12$, $r^2 = 0.746$) and ripe fruit consumption ($P = 0.009$, $N = 12$, $r^2 = 0.74$). In general, ripe fruits were the most consumed item through time, but, in periods of low fruit availability (January, and August–

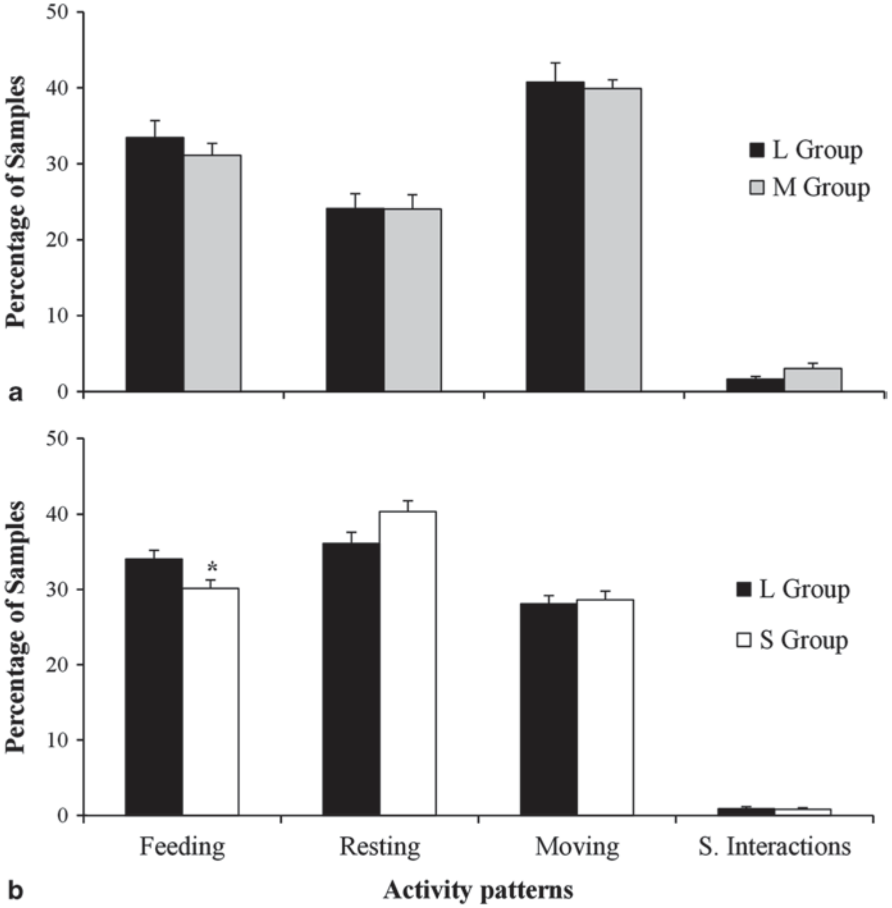

Fig. 13.2 Between-group comparison of the percentage of instantaneous samples registered for each of the different activities (error bars = standard error). (**a**) L group vs. M group: compared between January and April, (**b**) L group vs. S group: compared between May and December. The asterisk (*) above an activity denotes significant differences (*T* test for two independent samples; $p<0.05$)

October), woolly monkeys tended to increase their consumption of secondary items such as leaves and flowers (Fig. 13.4). However, fruit production was not a good predictor of leaf or flower consumption ($P=0.68$, $N=12$, $r^2=0.132$; $P=0.27$, $N=12$, $r^2=-0.34$, respectively).

The population of woolly monkeys in the fragment used a total of 229 plant species of 130 genera in 55 families. They used 133 species for fruit consumption (65 % of the total feeding time), 4 for seeds (8.0 %), 116 for leaves (17.5 %), 25 for flowers (8.5 %), and 11 for other parts (1.9 %). The most important species used for ripe fruit were *Ampelocera edentula* (13 %; Ulmaceae), *Spondias mombin* (5.0 %; Anacardiaceae), *Iriartea deltoidea* (4.0 %; Arecaceae), *Cecropia sciadophylla* (3.5 %; Urticaceae), and *Brosimum acutifolium* (3.2 %; Moraceae; Table 13.2). The

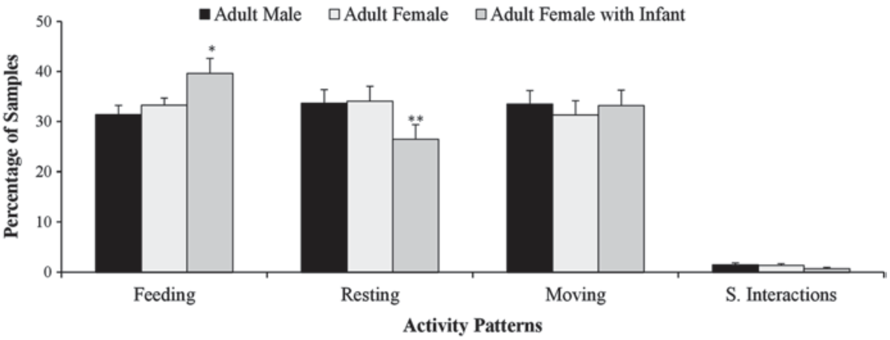

Fig. 13.3 Comparison of the percentage of instantaneous samples assigned to the different activities for each age/sex class in the L group (error *bars* show the standard error). An asterisk (*) above an activity denotes significant differences and the dash (−) shows a *P* score of 0.05 (*Z* test for two proportions)

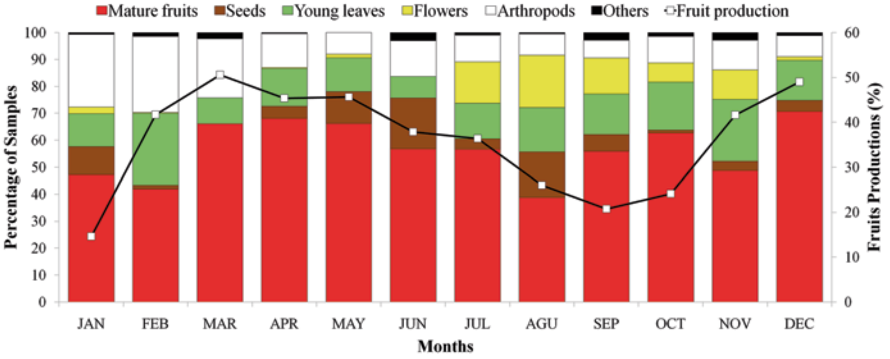

Fig. 13.4 Temporal variation in diet composition for woolly monkeys at the studied fragment (Guaviare, Colombia). We treated as an outlier the fruit production of a single individual of *Ficus pertusa* that generated a large peak in August

most important families in terms of feeding time on unripe fruits or seeds were Malvaceae (49.7 %), Moraceae (46.3 %), and Bignoniaceae (3.1 %). When comparing the plant families used by the three groups, Moraceae and Fabaceae were the most common for all groups. However, there was variation in the use of plant genera and species among groups. *Theobroma cacao* and *Pseudolmedia hirsuta* were the more-used species for group L, *Dialium guianense* and *Virola peruviana* for group M, and *Ampelocera edentula* and *Spondias mombin* for group S.

13.3.2 Use of Space and Degree of Cohesiveness

The average distance traveled per day for the population of woolly monkeys in the fragment was 2,339 m (range 784–4,841 m). We did not find significant differences between groups (group L vs. M: $t = -0.481$, df = 8, $P = 0.642$; group L vs. S:

Table 13.2 List of the ten most used dietary items for woolly monkeys in a forest fragment in Guaviare (Colombia) at the family, genus, and species levels

Family	Feeding time (%)	Species	Feeding time (%)
Fruits			
Moraceae	25.8	*Ampelocera edentula*	12.8
Ulmaceae	12.8	*Spondias mombin*	4.9
Fabaceae	12.2	*Iriartea deltoidea*	3.8
Urticaceae	8.6	*Cecropia sciadophylla*	3.5
Burseraceae	7.3	*Brosimum acutifolium*	3.5
Anacardiaceae	4.9	*Dialium guianense*	3.2
Arecaceae	4.9	*Byrsonima crispa*	2.8
Melastomataceae	4.2	*Ficus obtusifolia*	2.5
Malphigiaceae	2.8	*Crepidospermum rhoifolium*	2.3
Myristicaceae	2.7	*Genipa americana*	2.0
Seeds			
Malvaceae	50.6	*Theobroma cacao*	49.7
Moraceae	46.3	*Pseudolmedia hirsuta*	46.1
Bignoniaceae	3.1	*Arrabidaea verrucosa*	3.1
		Undetermined	0.9
		Perebea xanthochyma	0.2
Leaves			
Fabaceae	44.5	*Inga alba*	15.4
Moraceae	14.3	*Inga* cf. *laurina*	9.5
Melastomataceae	7.6	*Celtis iguanaeus*	7.4
Cannabaceae	7.4	*Pseudolmedia hirsuta*	6.1
Bignoniaceae	5.5	*Brosimum guianense*	4.2
Caricaceae	3.8	*Jacaratia digitata*	3.8
Cucurbitaceae	2.4	*Miconia affinis*	3.7
Araliaceae	2.2	*Inga* cf. *striolata*	2.9
Apocynaceae	1.9	*Henriettella sylvestris*	2.8
Sapindaceae	1.2	*Inga* cf. *capitata*	2.8
Flowers			
Bignoniaceae	48.1	*Arrabidaea verrucosa*	29.9
Arecaceae	21.1	*Astrocaryum chambira*	21.1
Fabaceae	12.0	*Arrabidaea nicotianiflora*	13.4
Moraceae	9.6	*Pseudolmedia hirsuta*	6.3
Ulmaceae	2.3	*Inga edulis*	6.0
Undetermined	2.0	*Acacia polyphylla*	4.7
Violaceae	1.6	*Pseudolmedia laevigata*	3.3
Urticaceae	1.0	*Arrabidaea* cf. *platyphylla*	2.9
Euphorbiaceae	0.7	*Ampelocera edentula*	2.3
Caricaceae	0.6	*Leonia glycycarpa*	1.6

$t = -0.772$, df $= 8$, $P = 0.462$). However, there was a tendency to find shorter daily traveled distances for the smallest group (L: 2,306 ± 812 m; M, 2,777 ± 909 m; S: 2,169 ± 529 m). Overall, the L, M, and S groups used a total of 72, 55, and 48 ha, respectively (128 ha of total area; Fig. 13.1b). This seems to reflect the number

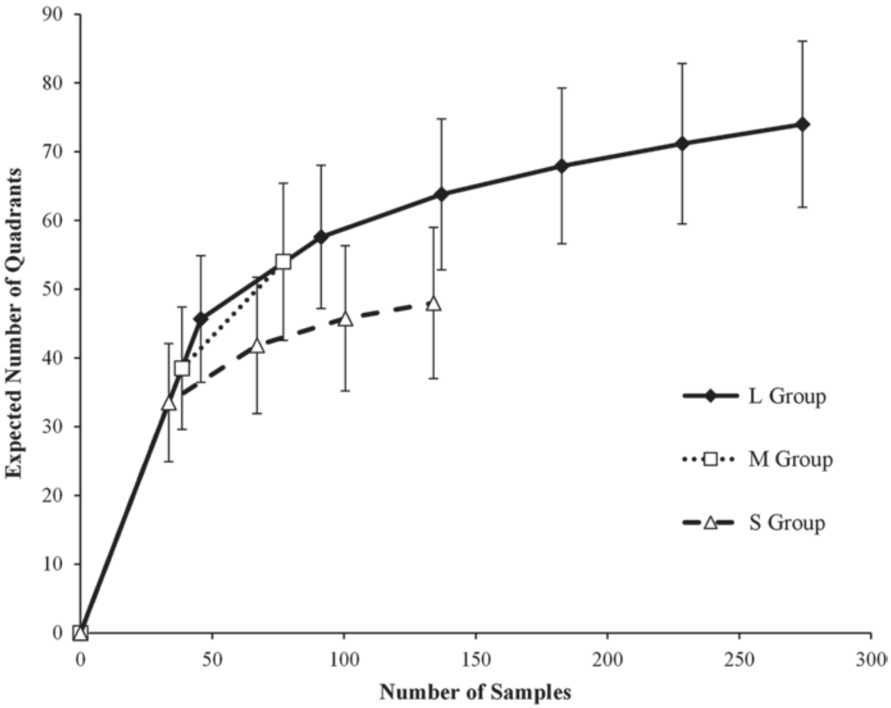

Fig. 13.5 Estimated home-range area used by woolly monkeys as a function of cumulative sampling effort. Sampling time differed for the three groups (L group, 12 months; M, 4 months; and S, 8 months). Error *bars* show a confidence interval of 95 % from several random iterations

of samples obtained for each group. In fact, the home range for the three groups increased as sample size increased and it did not reach an asymptote for any of the groups (Fig. 13.5). Finally, group L showed the highest interindividual separation compared to the other groups (Fig. 13.6; Kolmogorov–Smirnov test: L group: 96.3 ± 45 m vs. S group: 64 ± 16 m, $D = 2.34$, $P < 0.01$; L group: 72.9 ± 22 m vs. M group: 31.2 ± 21 m, $D = 5.23$, $P < 0.01$).

13.4 Discussion

13.4.1 Intraspecific Comparisons

In general, our results are within the ranges reported for other populations of woolly monkeys in undisturbed habitats (Di Fiore and Campbell 2007; Table 13.3). This indicates that woolly monkeys are in fact capable of inhabiting forest fragments, but their persistence is possibly not related to an extraordinary ecological or behavioral

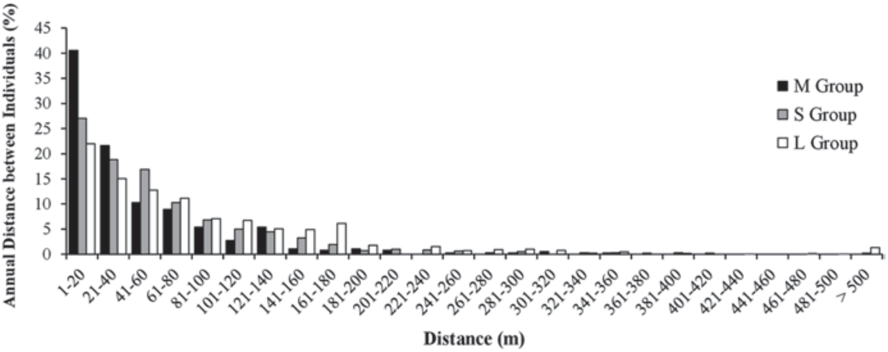

Fig. 13.6 Interindividual distance for three woolly monkey groups inhabiting a forest fragment in Guaviare (Colombia)

plasticity because the conditions at the fragment are adequate for the maintenance of the population. In fact, our annual fruit production estimate (685 kg/ha) turned out to be higher than the one calculated for an undisturbed site in Colombian Amazonia using the same methodology (Estación Biológica Caparú: interannual range = 106–471 kg/ha; González and Stevenson 2009; Vargas and Stevenson 2009). This seems to be a consequence of the low fertility of soils at Caparú (Defler 1995).

We found similar activity budgets for woolly monkeys in the fragment with Caparú (González and Stevenson 2009), where fruit production and population density are lower (Palacios and Peres 2005). In Tinigua, which has richer soils, it has been estimated that fruit production is the highest reported using our method (636–1,129 kg/ha, Stevenson, unpublished). In Tinigua, despite the high density of woolly monkeys, these rest for long periods of time and still show high feeding rates (Stevenson 2006). These comparisons suggest that activity budgets may be determined by feeding needs, which depend on resource availability and competition. Therefore, where fruit supply is low and/or frugivore population densities are high, woolly monkeys should travel more to get enough resources.

Tutín (1999) and Riley (2007) compared the effect of fragmentation on *Cercopithecus cephus* and *Macaca tonkeana,* respectively and found that these monkeys compensate the reduction of space and low productivity in a fragment by increasing insect and leaf consumption rates. In our case, we found that the consumption of leaves and flowers is in the upper range of the reported values for the genus, while the consumption of insects was not substantially different from the one reported for continuous forests (Table 13.3b). Diet composition was similar to the one found at Caparú (González and Stevenson 2009). This suggests that medium fruit production levels and high population density promote the search for secondary items to compensate for the lack of preferred items. Then, the feeding behavior becomes similar to the one in places with lower resources, but with a low population density.

When comparing fruit diet composition of woolly monkeys at different study sites (Stevenson et al. 1994; Peres 1994; Defler and Defler 1996; Di Fiore 2004;

Table 13.3 Comparison of the behavior of woolly monkeys at different study sites: (a) activity patterns, (b) use of dietary items (fruits and seeds items were grouped in a single category, since this allows for direct comparisons with other studies), and (c) daily traveled distance and home range

a) Site (reference)	*Feeding (%)*	*Resting (%)*	*Moving (%)*	*S. Interactions (%)*
Yasuni NP (Di Fiore and Rodman 2001)	36.2	23.2	34.5	6.1
Caparu BS. (Defler 1995)	25.8	29.9	38.8	5.5
Tinigua NP. (Stevenson 2006)	36	35	26	3
Caparu BS (González and Stevenson 2009)	18	50	29.5	2.5
El Trueno Fragment (this study)	31.7	32.4	34.2	1.8
b)	*Fruits (%)*	*Leaves (%)*	*Arthropods (%)*	*Others (%)*
Caparu BS. (Defler and Defler 1996)	84	11	4	1
Urucu (Peres 1994)	81	16	0.1	3
Yasuni NP. (Di fiore 2004)	77	8	13	2
Caparu BS. (González and Stevenson 2009)	69	16	13	2
Tinigua NP. (Stevenson 2006)	59	13	25	3
El Trueno Fragment (this study)	62.3	15.5	15.8	6.3
c)	*Daily traveled distance (m)*		*Home range (ha)*	
Caparu BS. (Defler 1996)	2,880		760	
Urucu (Peres 1996)	–		935	
Yasuni NP (Di Fiore 2003)	1,792–1,878		108–124	
Caparu BS. (González and Stevenson 2009)	2,539–2,125		>440	
Tinigua NP. (Stevenson 2006)	2,001		173	
El Trueno Fragment (this study)	2,339		126 (76–55–48)	

Our values in this table (this study) represent the average for the three groups

Stevenson 2006), we found that woolly monkeys in our study fragment share two of the three most important plant families used by woolly monkeys at other sites (Moraceae and Fabaceae). However, the third most used family in the fragment (Ulmaceae) had not been previously identified as an important resource in their diet. At the species level, two of the most used species *Ampelocera edentula* (Ulmaceae) and *Theobroma cacao* (Malvaceae) had not been reported in the diet of the woolly monkeys previously. These results may be explained by the fact that fruit production of *A. edentula* coincided with the months of overall low fruit productivity (September–October), and to the fact that the fragment has a plantation of *T. cacao*. This shows that woolly monkeys can exhibit an opportunistic behavior, and may compensate to some degree for the variation in the preferred fruit available with other non-preferred items. For instance, *T. cacao* in Tinigua may show high fruit production, but it has never been reported in the diet of woolly monkeys inhabiting undisturbed forests (Stevenson 2002).

The average daily travel distance and home range of woolly monkeys at the fragment are within the reported range for the genus (Table 13.3c). The average travel distance resembles the one reported by Defler (1996) in Caparú, while the home range area is similar to the one found in places with higher soil fertility (Stevenson et al. 1994; Di Fiore 2003). The relatively small home range area found in the fragment seems to reflect the restrictions imposed on populations that inhabit a small forest remnant. Defler (1996) suggested that soil fertility is the main factor explaining such variation. In other words, the large home ranges that woolly monkeys exhibit at Caparú would be a result of areas with poor soils, lower fruit production, and the need to travel more to reach nutritional demands. For example, Tinigua has fertile soils and high fruit production, and the home range of woolly monkeys is close to 200 ha and the mean daily traveled distance is 2,000 m (Stevenson 2006). Stevenson et al. (1994) suggested that such a pattern is explained by the high productivity of the forest, where woolly monkeys do not need to travel great distances to access their preferred resources. All this suggests that home ranges and daily traveled distances of woolly monkeys inhabiting a forest fragment are mainly a result of fruit production and fragment size.

13.4.2 Intrapopulation Comparisons

We found few differences in activity budgets and diet composition among groups. However, arthropod feeding was more frequent in group M than in group L. We suggest that this difference represents higher arthropod availability in the core areas of group M. In addition, we found a higher feeding frequency in individuals of group L compared to individuals of group S. We suggest the high number of births in group L at the end of the study ($n=11$) might have caused an increase in nutritional demands for the females. It has been estimated that protein and mineral consumption in pregnant and lactating females may increase about 25 and 50 %, respectively, in primates (Coelho 1974; Altmann 1980). This is also consistent with the result showing that females with infants tend to ingest more leaves than females without infants; however, other patterns have been observed in other woolly monkey populations (Stevenson 2006). Nonetheless, in other primate's species (e.g., lemurs) during lactation the females ingest a high proportion of young leaves in order to acquire calcium and protein, as well as some energy, which would be crucial for offspring development (Sauther 1998).

During periods of high fruit production (February–July and November–December), woolly monkeys in the fragment moved more and fed mainly on ripe fruits. However, when productivity was low (September–October), woolly monkeys did not move lesser than in periods of high productivity. This pattern does not support a hypothesis of energy minimization during food scarcity periods (Rosenberger and Strier 1989), but it is similar to previous findings for woolly monkeys in Caparú (González and Stevenson 2009). We observed long daily travel distance and repetitive circuits on a single day, in spite of relatively short distances among fruit resources. Thus, we believe that in periods of fruit scarcity woolly monkeys maintain the same movement frequency because they forage for alternative resources such as leaves and insects.

Initially, it was described that woolly monkeys lived in fission–fusion groups similar to *Ateles* and *Brachyteles* (e.g., Terborgh and Janson 1986), smaller group units allowing for a reduction in intragroup competition (Symington 1988). However, at least in one site, woolly monkeys live in much more cohesive groups than sympatric spider monkeys (Stevenson et al. 1998). It has been proposed that arthropod feeding may have relaxed the negative effects of food competition, leading to the evolution of a more cohesive social structure in *Lagothrix* (Stevenson et al. 1994). However, Stevenson and Castellanos (2000) found that intragroup competition for fruits is an important limiting factor in determining foraging group size. In our study, the largest group showed a higher spatial separation among its individuals compared to the other two groups (Fig. 13.6). It is probable that, similar to what was found for *Propithecus diadema* in Madagascar (Irwin 2007), woolly monkeys at the fragment reduce competition by increasing intragroup distance. Thus, our results support the idea that woolly monkeys living in a forest fragment could reduce intragroup competition for food, by reducing their cohesiveness. However, groups with many individuals must compensate for their size by traveling longer distances or by increasing foraging distances (Janson and Goldsmith 1995; Stevenson 2006; but see Chapman and Chapman 2000), which was not evident in our study, probably due to a small sample size for the M group.

13.4.3 Implications for Conservation

Our study suggests that woolly monkeys do not exhibit drastic behavioral changes in response to fragmentation. Similar to what has been reported for undisturbed habitats, woolly monkeys at the studied fragment adjusted their behavioral patterns mainly as a response to primate density and resource availability. Even though woolly monkeys consumed non-preferred items in the remnant, our study suggests that their populations show low behavioral plasticity. Thus, their persistence in the remnant seems to be determined by favorable conditions met in the fragment, and not by a particular behavioral response. This suggests that a higher reduction in resources and the loss of space can affect their survival. We suggest that woolly monkeys are rarely found in fragmented forests because: (1) Remnants may not be productive enough to sustain the populations, which can be a result of their small size and/or low fertility; and (2) fragmentation may be associated with an elevated hunting rate (Peres and Palacios 2007), which would be the main negative effect for woolly monkey populations at fragments with sufficient resource production (which should include arthropod abundance and foliage quality, as well as fruit production).

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Appendix 13.1

Statistical comparisons of activity (a), and diet (b), between different age/sex classes in three groups of woolly monkeys inhabiting a fragment in Colombian Amazonia. The monthly variation in diet is also shown (c; adult male = AM; adult female = AF; adult female dependent infant = AFI)

	L group	M group	S group
Activity budgets among age/sex classes (Z test for two proportions: ANOVA and Kruskal–Wallis test)			
Feeding			
AM vs. AF	$Z=0.657$; $P=0.453$	$Z=0.495$; $P=0.582$	$Z=-0.207$; $P=0.802$
AM vs. AFI	$Z=2.689$; $P=0.006$*	$Z=0.385$; $P=0.652$	$Z=0.129$; $P=0.880$
AF vs. AFI	$Z=2.085$; $P=0.031$*	$Z=0.892$; $P=0.395$	$Z=0.369$; $P=0.652$
Resting			
AM vs. AF	$Z=-0.061$; $P=0.960$	$Z=0.644$; $P=0.515$	$Z=0.866$; $P=0.342$
AM vs. AFI	$Z=1.857$; $P=0.062$	$Z=-0.178$ $P=0.802$	$Z=0.173$; $P=0.802$
AF vs. AFI	$Z=1.86$; $P=0.051$	$Z=0.46$; $P=0.582$	$Z=0.424$; $P=0.652$
Moving			
AM vs. AF	$Z=0.657$; $P=0.453$	$Z=0.579$; $P=0.515$	$Z=0.489$; $P=0.582$
AM vs. AFI	$Z=-0.076$; $P=0.960$	$Z=-0.429$; $P=0.0.652$	$Z=0.138$; $P=0.880$
AF vs. AFI	$Z=0.514$; $P=0.582$	$Z=-0.116$; $P=0.880$	$Z=0.138$; $P=0.880$
I. Socials	$F=0.26$; df=2; $P=0.26$	$F=1.13$; df=2; $P=0.36$	$X^2=1.50$; df=2; $P=0.17$
Diet composition between the age/sex classes (Z test for two proportions)			
Mature fruits			
AM vs. AF	$Z=0.416$; $P=0.652$	$Z=0.396$; $P=0.652$	$Z=0.730$; $P=0.453$
AM vs. AFI	$Z=1.32$; $P=0.177$	$Z=0.261$; $P=0.726$	$Z=0.591$; $P=0.582$
AF vs. AFI	$Z=1.759$; $P=0.080$	$Z=-0.166$; $P=0.802$	$Z=-0.139$; $P=0.880$
Seeds			
AM vs. AF	$Z=0.626$; $\mathrm{P}=0.515$	–	–
AM vs. AFI	$Z=0.844$; $\mathrm{P}=0.359$	–	–
AF vs. AFI	$Z=0.301$; $\mathrm{P}=0.726$	–	–
Young leaves			
AM vs. AF	$Z=0.147$; $P=0.880$	$Z=-0.339$; $P=0.726$	$Z=0.148$; $P=0.880$
AM vs. AFI	$Z=1.112$; $P=0.250$	$Z=-0.198$; $P=0.802$	$Z=0.460$; $P=0.582$
AF vs. AFI	$Z=1.436$; $P=0.147$	$Z=-0.259$; $P=0.726$	$Z=0.075$; $P=0.880$
Arthropods			
AM vs. AF	$Z=-0.293$; $P=0.802$	$Z=0.199$; $P=0.802$	$Z=-0.187$; $P=0.802$
AM vs. AFI	$Z=0.185$; $P=0.802$	$Z=0.075$; $P=0.880$	$Z=-0.144$; $P=0.880$
AF vs. AFI	$Z=0.2$; $P=0.802$	$Z=-0.262$; $P=0.726$	$Z=-0.366$; $P=0.652$

Flowers			
MA vs. FA	$Z=0.207$; $P=0.802$	–	$Z=-0.380$; $P=0.652$
MA vs. FAI	$Z=0.123$; $P=0.0.880$	–	$Z=-0.545$; $P=0.582$
FA vs. FAI	$Z=-0.382$; $P=0.726$	–	$Z=-0.435$; $P=0.652$
Temporal variation in diet composition (ANOVA and Kruskal–Wallis test)			
Mature fruits	$F=4.678$; $df=11$; $P=0.001$*	$F=2.778$; $df=3$; $P=0.075$	$F=4.351$; $df=7$; $P=0.002$*
Seeds	$F=4.703$; $df=11$; $P>0.001$*	–	$X^2=11.865$; $df=7$; $P=0.105$
Young leaves	$F=2.351$; $df=11$; $P=0.021$*	$F=1.232$; $df=3$; $P=0.331$	$F=1.679$; $df=7$; $P=0.150$
Arthropods	$F=3.418$; $df=11$; $P=0.001$*	$F=1.039$; $df=3$; $P=0.402$	$F=0.580$; $df=7$; $P=0.767$
Flowers	$F=4.309$; $df=11$; $P>0.001$*	–	$F=2.956$; $df=7$; $P=0.017$*

* Significant differences

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Part V
Conservation

Chapter 14
Notes on the Behavior of Captive and Released Woolly Monkeys (*Lagothrix lagothricha*): Reintroduction as a Conservation Strategy in Colombian Southern Amazon

Juan F Millán, Sara E Bennett and Pablo R. Stevenson

Abstract Woolly monkeys (*Lagothrix lagothricha*), one of the largest primates in the neotropics, play important roles as seed dispersers in neotropical forests. All subspecies hold some kind of threatened status (VU, vulnerable, and CR, critically endangered) according to International Union for Conservation of Nature, mainly due to deforestation, subsistence hunting, and illegal wildlife trade. Therefore, a high number of animals are kept in rescue centers and zoos, where conditions tend to be poor and their survival is low. This study's main purpose was to compare the activity budget of free-ranging woolly monkeys, captive animals at a rescue center, and a group of rehabilitated and released monkeys. Results showed an important difference between the time budget of captive and wild monkeys, while showing an intermediate pattern for the released group. Our results suggest that rehabilitation and release imply high mortality rates, but may be an effective strategy for woolly monkey conservation.

Keywords Woolly monkeys · *Lagothrix lagothricha* · Amazon · Rehabilitation · Behavior

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J. F. Millán (✉)
Laboratorio de Ecología de Bosques Tropicales y Primatología,
Departamento de Ciencias Biológicas, Universidad de Los Andes,
Bogotá and Fundación Maikuchiga, Bogotá, Amazonas, Colombia
e-mail: juanfer77@hotmail.com

S. E. Bennett
Fundación Maikuchiga, Bogotá, Amazonas, Colombia
e-mail: nomiosarabennett@yahoo.com

P. R. Stevenson
Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia
e-mail: pstevens@uniandes.edu.co

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14.1 Introduction

Habitat destruction and hunting pressure are among the main threats for large forest mammals. Woolly monkeys (*Lagothrix*) are a preferred game species due to their large size (Peres and Palacios 2007) and, in most cases, females with associated offspring are targeted to take double profit from the kill, as the offspring can be kept or sold as pets (Rodríguez-Mahecha et al. 2006). These pressures have resulted in the decrease of wild populations all through the historic distribution, to the extent of becoming locally extinct in some areas (Hernandez-Camacho and Cooper 1976; Stevenson and Aldana 2008). In Colombia, two subspecies of woolly monkeys are found: *Lagothrix lagothricha lagothricha* and *L. l. lugens* (Botero et al. 2010). The original distribution of *Lagothrix* included a great part of the Orinoco Basin, the Amazon Basin, and some areas in Central and Eastern Andean mountains (Defler 2004). The local extinction and decrease of woolly monkey population densities has been identified as a problem due to their ecological importance as seed dispersers (Stevenson 2011). Colombian woolly monkeys (*Lagothrix lagothricha lugens*) at Tinigua National Park were found to disperse almost 1 million seeds per square km each day, resulting in a number similar to those dispersed by all the avian species in the same study site (Stevenson 2007). It has been demonstrated that the absence or decrease in the populations of woolly monkeys and other atelines results in lower diversity in plant regeneration (Nuñez-Itauri and Howe 2007; Stevenson 2011). In fact, hunting tends to change the composition of plants recruiting in neotropical forests (Terborgh et al. 2008).

Woolly monkeys captured as newborns or juveniles often fall victims to illegal wildlife trade and are kept as pets under conditions that differ greatly from their natural environment. In some cases, these animals are confiscated by environmental authorities and sent to rescue centers, assessment and release centers, and zoos where they suffer high mortality rates due to stressful conditions (Hosey 2005). Very few ex situ woolly monkey colonies have been maintained for long periods of time because of medical problems such as diabetes and hypertension (Ange-van Heugten et al. 2008).

Even though many studies show that enriched enclosures simulating natural conditions may enable natural behavior in primates (Hancocks 1980; Redshaw and Mallinson 1991; Maple and Finlay 1989; Buchanan-Smith et al. 2004; Melfi 2005; Guzman-Caro and Stevenson, this volume), there are strong limitations as to how closely the natural environment can be simulated. In natural conditions, woolly monkey groups have extensive home ranges (170–800 ha, Defler 2004) and long daily movement (ca. 2 km, Stevenson 2006).Therefore, it is a great challenge to recreate captive conditions in which woolly monkeys could show natural behavior. In consequence, captivity generates not only behavioral changes but also psychological disturbances (Hosey 2005) and even physiological problems leading to the development of diseases (Ange-van Heugten et al. 2008).

The main objective of this study was to show how much behavior patterns differ among captive, rehabilitated groups, and wild populations. This behavioral study may provide insight on how rehabilitation can be accomplished in woolly monkeys, even though it is a long and complicated process that deals with many variables ranging from individual behavior (Jones 2005) to ecological forest dynamics. Rehabilitation can be difficult, depending on how human dependent on individual becomes, due to the effects of captivity (however, here we show that this dependency can also have positive effects). Previous experience in the rehabilitation of several woolly moneys at Caparú Biological Station in Vaupés by the third author convinced us that rehabilitation was possible.

Another great limitation in woolly monkey rehabilitation is the use of vertical space. Woolly monkeys are strictly arboreal with preferred heights ranging from 12 to 18 m, and they seldom descend to the ground level (Stevenson and Quiñones 1993). Contrastingly, monkeys kept as house pets, in cages or enclosures, spend a great amount of time on the floor, a behavior that in a natural environment would put them at great risk of predation. After release, monkeys also have to learn to recognize food and other resources in the forest in order to survive after human care has phased out. Finally, one of the most complicated issues during rehabilitation processes is human–monkey attachment, which might take a long time to break.

14.2 Methods

Captive woolly monkeys were sampled at CORTOLIMA's animal attention and assessment center (CAV acronym in Spanish) located on the outskirts of Ibague, Tolima (Colombia). The group of five *Lagothrix lagothricha* individuals was made up of two subadults (male and female) and, in a separate cage, two juveniles (male and female) and an infant male. Monkeys were kept in very small cages (Fig. 14.1) with very little enrichment. Animals kept at this center were either confiscated by environmental authorities or voluntarily offered by owners. These centers (CAVs), administered by local environmental authorities, are meant to assess animals that are brought into their custody, provide them with necessary health treatment, rehabilitate them, and finally aim for their release as a definite solution. Unfortunately, in most cases, the solution ends up being indefinite confinement due to the lack of opportunities for release. Individuals are kept under the care of veterinarians and other specialists to ensure their welfare; however, most centers are underfunded and do not have the proper facilities or staff training to keep the animals under adequate conditions, which often results in high mortality rates.

From the time when this center was first visited (October 2010) to the time when the data were collected (May 2011), both health and behavior seemed to have deteriorated, possibly due to captivity-related stress. At the end of the project, three of the monkeys had died due to severe intestinal infections. Historical mortality rates at this center could not be calculated for the species because the center's staff did not provide this information. This case exemplifies the critical situation faced by captive populations throughout the country and, thus, shows the need to develop

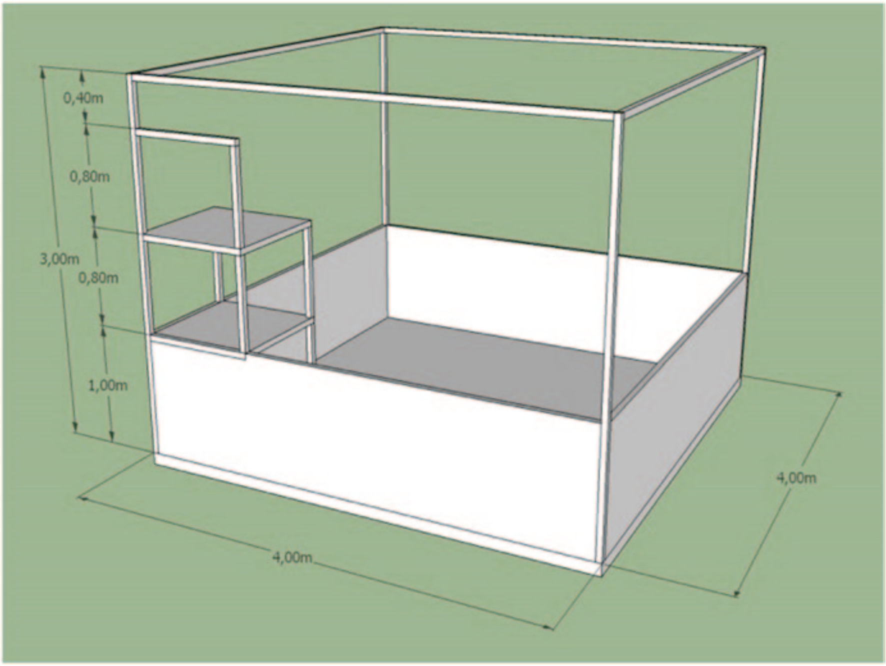

Fig. 14.1 Primate enclosure at rescue center

rehabilitation and release programs to ensure species' survival after assessment and medical care has been provided at the rescue centers.

A group of rehabilitated and released woolly monkeys was sampled at Amacayacu National Park, Amazonas (3°48′02″ S 70°15′18″ W). Monkeys from this group were kept as pets at some point and were given to the Maikuchiga project to be rehabilitated and released as an alternative to captivity at a rescue center in Leticia, Amazonas, Colombia. This group will be referred to as "semi-wild." When the first data from this group were collected in April 2011, the group was made up of six monkeys: two adult females, one subadult female, two juvenile females, and one adult male. When the second set of data was collected in August and September 2012, the group had lost three females and, thus, data were collected from the surviving male and two females, an adult and a former juvenile, now a subadult. One of the two missing females (adult) died from unknown causes, and the other one (subadult) was rescued and taken back to the "Animal House" (rehabilitation facility) due to poor health, while a juvenile was unaccounted for.

These monkeys started a rehabilitation process around 2006 and were released in 2010, in an isolated area away from contact with tourists and visitors. Additionally, there is an agreement with indigenous communities, banning primate-hunting activities. The origins of the group's individuals are unknown because they were confiscated around Leticia, Amazonas, and molecular tests have not been carried out.

Fig. 14.2 Base 2 release and monitoring station of woolly monkeys in Amacayacu National Park

For the monkeys' release, a station (Base 2) was built in order to monitor, feed, and complete a gradual release, slowly phasing human care out. The station had five feeding platforms and a facility for two researchers or keepers. Monkeys were fed at this location three times a day during the first months, and were then gradually induced to forage on their own. Human–monkey interactions were also gradually phased out to allow monkeys to become more independent and self-sufficient. During the second sampling, the group was completely independent until the male became extremely ill and had to be rescued and taken back to the station for monitoring and care to ensure his survival. During this time, the two remaining females also approached the station looking for food and were fed by humans very much like when they were first released. This situation represents one of the major drawbacks that rehabilitation and release processes may face, where a few steps backward have to be taken to ensure the group's survival and viability, facing a trade-off between survival and independence (Fig. 14.2).

To collect data on activity, diet, and vertical space use, focal individuals were followed throughout the day, in the same way as it has been used for natural populations (Stevenson 2006). For the captive group, data were collected from observations made from a safe distance from the cage to reduce human–monkey interactions. Four-day samplings were conducted for every individual in the group. Four of the observed individuals died shortly after data were collected. The same methods were used for the semi-wild group, following the group for an average of 10 h per day, for a total of 10 sampling days on April 2011 and 16 sampling days in August–September 2012.To calculate the home range, reference points were taken during sampling days using a global positioning system (GPS) device and then mapped to determine the semi-wild group's ranging area by the convex polygon method.

The semi-wild group sampling on 2011 will be from here on referred to as "semi-wild1" and sampling from 2012 will be referred to as "semi-wild2." The first sampling *semi-wild1* was done during the peak of the rainy season when most of the forest was flooded; while the sampling done in 2012 (*semi-wild2*) was done during

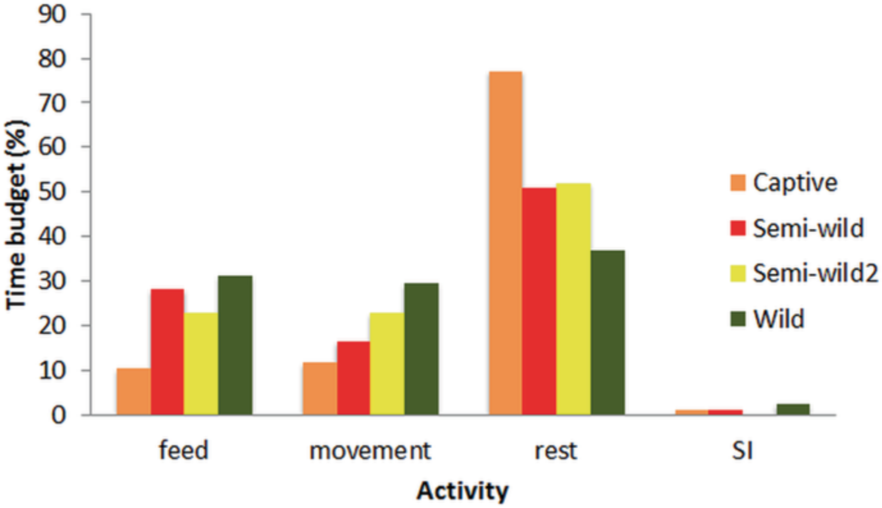

Fig. 14.3 Comparison of the activity budget for woolly monkeys living in captive, semi-wild, and wild conditions. *SI* social interactions

the driest period of the year and one of the lowest points of forest productivity (J. Millan, pers. observations). In all cases, instantaneous samples were taken every 10 min, registering activity (feeding, movement, resting, and social interactions) and height. The feeding category was separated into different feeding types: leaves (including other vegetative plant parts), arthropods, flowers, fruits, and others. Data from wild populations were gathered from the following studies and locations: Stevenson (2006), Tinigua National Park (Meta, Colombia), and Vargas et al. (2014), Huila, Colombia.

To show the influence of the conditions (captive, *semi-wild1, semi-wild2,* and wild) over the time budget for each activity, a Kruskal–Wallis test was performed to show differences among conditions. For the analysis of the differences in activity budgets between conditions, Tukey's test was performed.

14.3 Results

Behavioral analyses showed marked differences among the three groups, especially between the captive and wild populations. The Kruskal–Wallis analyses showed significant differences for all four activities evaluated (movement, resting, social interactions, and feeding). As was expected, the semi-wild group showed intermediate behavior patterns, except for social interactions that were highest in captivity and lowest in the released group. However, social interactions were not frequent and the main activities showed intermediate patterns in the released population. Even more, there was a tendency toward wild behavior patterns between sampling periods in the released group (Fig. 14.3).

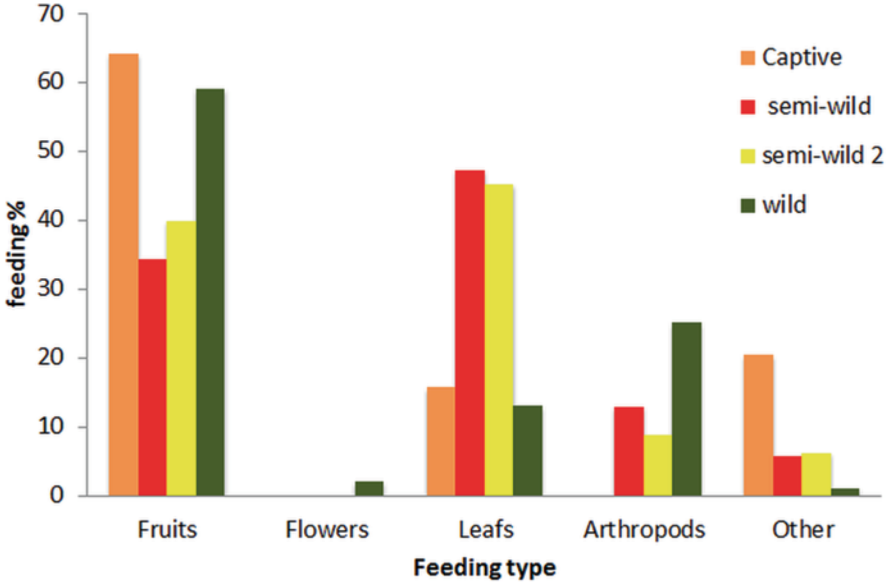

Fig. 14.4 Diet of woolly monkeys in captive, semi-wild, and wild conditions

The largest difference in activity budgets was found in resting ($X^{2=}55.2$, df. = 2, $p < 0.001$), because captive monkeys engage in this behavior much more often (77.0 %) than wild groups (36.9 %). The *semi-wild1* and *semi-wild2* groups showed an intermediate value (50.9 and 51.9 %). In the movement category, a large difference was found between captive and wild monkeys (11.6 % vs. 29.4 %), while the semi-wild group showed an increase of 6.3 % in time invested in moving during the second sampling, which suggests an improvement toward wild behavior patterns. All three treatments showed differences in a posteriori Tukey tests. We also observed differences in movement among conditions ($X^{2=}28.0$, df. = 2, $p < 0.001$), being on average highest in natural conditions and lowest in captivity. However, a posteriori analyses showed no differences between the released group and the groups in natural conditions ($p > 0.05$).

Feeding time budgets also showed an interesting increasing pattern going from conditioned scheduled feeding in captivity, to feeding reinforcement in semi-wild, and finally to natural foraging for *semi-wild2* and wild. Social interactions were infrequent in all cases, but particularly low for *semi-wild2* (0.2 %), probably indicating very few interactions among group members in food scarcity periods.

Differences were also found among the feeding budgets of the different groups ($X^{2=}32.4$, df. = 2, $p < 0.001$; Fig. 14.4). However, a posteriori analyses showed no differences between the released group and the groups in natural conditions ($p > 0.05$). In captivity, there is a strong relationship between consumption and what monkeys were offered, limiting feeding choice. In contrast, free-living (semi-wild and wild) monkeys have greatly different food alternatives and they show some feeding preferences (Stevenson 2004).

Captive monkeys were offered mostly fruit and the diet was enriched with protein-rich items such as hardboiled eggs, dog food, and raw meat. The semi-wild group was reinforced with enriched oatmeal balls (oats, honey, and soy milk) and fruits. This group also foraged in the forest as part of a self-learning process, often discarding different items. During the *semi-wild2* sampling, almost no reinforcement was offered despite the low forest productivity. Leaves seemed to be an important resource during both semi-wild samplings.

The feeding category classified as *other* was extremely diverse, including all sorts of nontypical food resources consumed by the different groups. For example, for captive monkeys, this category included items such as dog food, raw meat, and eggs; and for the semi-wild group, it included oatmeal balls and alternative forest resources such as different plant stems, shoots, seeds and, in one particular case, a frog. For wild populations, this category included roughly the same items as for the semi-wild group (Stevenson 2004; Defler 2004). This category was particularly important for the semi-wild group during the semi-wild2 sampling since, as they become more independent from human care, they explore different food alternatives. Interestingly, 45.5 % of the "leaf" category was made up of petioles from a Cyclanthaceae epiphyte.

Social interactions were the least frequent activities and there were significant differences among the three conditions($X^2 = 16.7$, df. = 2, $p = 0.002$). When the group was first released, there were far more observations on social behavior, probably due to all the space and resources shared by the group that made them spatially closer to each other. Actually, woolly monkeys in captivity usually show a higher rate of social interactions than in natural conditions (Guzman and Stevenson this volume). In our study, during the second phase, two grooming bouts were observed and strong aggression was seen from the adult female toward the subadult, while exploiting a fruited *Gustavia* tree.

In captivity, a subadult male and a female were kept in the same cage and social interactions were often observed, mostly grooming. However, at feeding times there was also strong aggression from the female toward the male. Aggression in captivity occurs most often because of stress and scarce resources. The juvenile male, the female, and the infant were kept in a separate cage. In this group, there were interactions between the female and the infant, often resulting in the female carrying the youngster around the cage. The juvenile male also displayed sexual behavior toward the female (Fig. 14.5).

Regarding vertical space use, there were large differences between captive and free-ranging monkeys, in part because cage height limits the maximum height preferred by monkeys (Figs. 14.6 and 14.7). Wild monkeys showed a preference for heights between 12 and18 m (Stevenson and Quiñones 1993), while both samples from the semi-wild group indicated a preference for the 0–6 m range. For *semi-wild1,* this was true as they spent a good amount of time on the forest floor mostly foraging for arthropods in the station's surrounding vegetation and also exploring floating vegetation for arthropods and other resources during the flooded season. During *semi-wild2,* although most of the data fit into this category (39.2 %), forest floor use was extremely low, only being recorded twice and certainly related to

Fig. 14.5 Adult female feeding on Cyclanthaceae petioles

monkey–observer interaction. The average height for this group was of 9.6 m, close to what is expected for wild populations. The use of the highest strata (>20) was limited in both groups.

During the second sampling week of *semi-wild2,* the male went missing and was found 2 weeks later in poor condition (Fig. 14.8). He had to be rescued and taken back to Base 2 in order to be monitored and fed on a regular basis to ensure his survival. No tests were done on the monkey, based on the assumption that he was malnourished instead of being sick. This completely altered data collection, because shortly after he was evacuated to Base 2, the two females joined him, and once again began to feed almost exclusively on human-provided food, spending long periods of time at ground level whenever people were present at the site. After 3 weeks of care, the male seemed to be recovering well and gaining weight. From this point on, food was left on platforms and monkeys were left to return to their more wild-like habits.

We estimated a home range of 350 ha for the semi-wild group. Points used to calculate the area were taken during sampling days, but observations on the group in different sites during monitoring activities were also taken into account for the analysis. It is possible that their home range could be larger than the sampled area and, therefore, further studies are needed to determine a more accurate home range.

14.4 Discussion

Our results show that woolly monkey behavior is highly influenced by the conditions faced by the monkeys, whether they are in captivity, semi-wild, or wild environment. This can be shown in the groups' time budget distribution for the different activities, and how this relates to space and other resources available for the group. We found that there was a gradient from captive to wild when considering the time used for the different activities. Furthermore, differences in behavior between the two data sets taken for the semi-wild group (2011 and 2012) were evident within

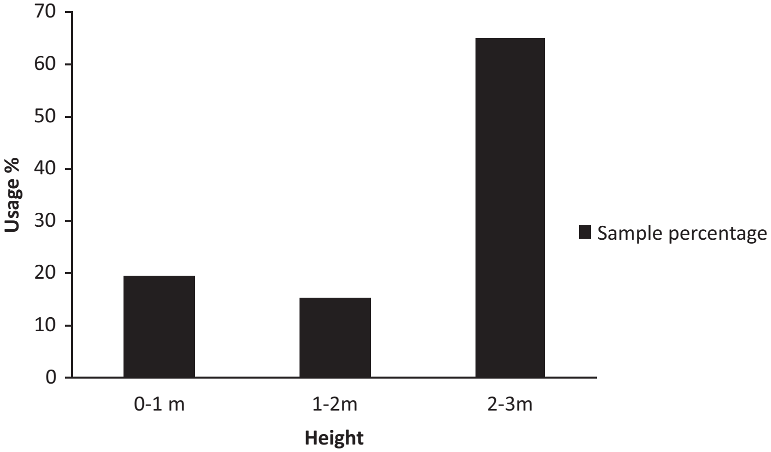

Fig. 14.6 Vertical space use in captivity

a year, thus suggesting a general tendency toward a higher resemblance to wild behavior patterns. For example, captive monkeys spend almost twice the amount of time resting compared to the wild group (77.0 % vs. 36.8 %). The extremely large amount of time captive monkeys spend resting may be related to the small size of their enclosure (roughly 48 m^3), and also to very poor environmental enrichment (i.e., individuals do not need to move to get resources). These cages are meant to be temporary enclosures and are not designed to permanently keep the primates. This often leads to a considerable restriction of movement, which can in turn lead to both physiological and psychological disorders like diabetes, hypertension, depression, and death, as seen with the group found at the rescue center. The percentage of time semi-wild monkeys spent resting (50.1 %) was intermediate to the values for captive and wild groups, suggesting an improvement toward wild behavior (Fig. 14.9).

In diverse forests such as those of the Colombian southern Amazon, food patches are located far apart from each other, forcing monkeys to move more than at less diverse and more productive forests (Gonzales and Stevenson 2010). However, moving patterns are also high in fragments (Zarate 2010) and the highest frequency of movement so far reported corresponds to a sub-Andean population (Vargas et al. 2014), where woolly monkeys spend much time looking for arthropods (mainly in epiphytic plants). Therefore, moving patterns in woolly monkeys seem to depend on different factors, such as the distribution, type, and abundance of resources, and this distribution is remarkably different in captivity. Interestingly, woolly monkeys spent 50 % of the time resting in the Estación Biológica Caparú (Vaupés, Colombia; Gonzales and Stevenson 2010), and this is very similar to the patterns found for the semi-wild group, both in highly diverse but low in terms of fruit production.

We think that the presence of observers could have influenced the behavior of the released group. For instance, when the group was first released, keepers and researchers would often lead the group into the jungle to get them used to their new home and stimulate movement and exploration by the group. Two weeks after the

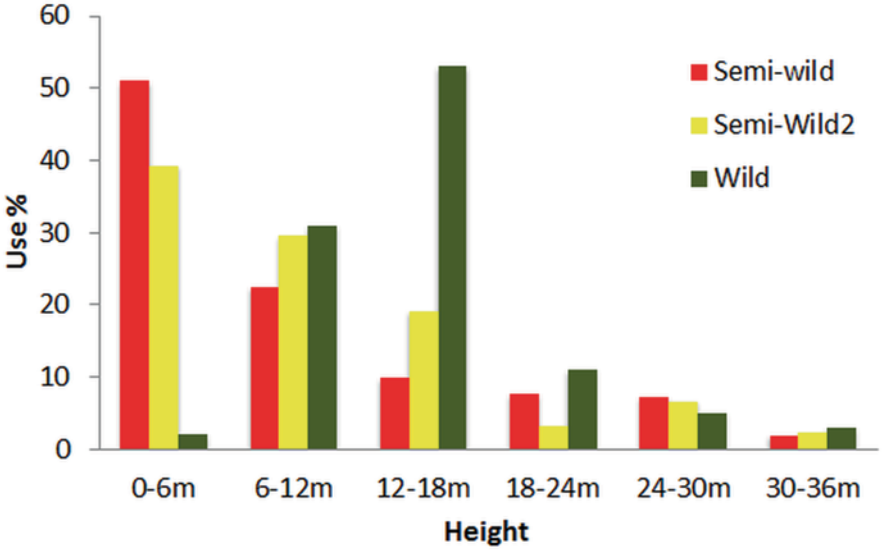

Fig. 14.7 Vertical space usage by wild and semi-wild free-living woolly monkeys

Fig. 14.8 Extremely ill adult male, Parce, on the floor. Parce was rescued and evacuated to Base 2 station

group was followed in 2012, we began to observe a decrease in the group's activity around 9:00 hours, when the two females climbed up to the highest branches and took long naps of up to 2 h. After several days of observing the same behavior, we

Fig. 14.9 Caged subadult male at the rescue center

Fig. 14.10 Difference in resting monkeys. Captive juvenile sleeping on the floor and adult semi-wild female sleeping on a branch at approximately 10 m

realized it was because they were waiting for the observers to lead them through the forest, or they probably expected food. When observers continued traveling at this time of the day in the next couple of days, the group followed us even to the point of ignoring commonly consumed fruiting trees (Fig. 14.10).

Compared to free-ranging monkeys (semi-wild and wild), captive monkeys invest a significantly lower amount of time in feeding. This can be explained by the fact that captive individuals are offered food only once a day in a regular schedule limiting feeding bouts to that moment of the day, which never lasts more than 40 min. Feeding patterns were quite different in both semi-wild and wild monkeys, since these can forage at any time and for as long as they want (Peres 1994; Stevenson 2006). Feeding preferences also differ depending on the group's environment. Captive monkeys for example are offered mostly fruits (64.0 %) based on the fact that wild woolly monkeys have a mostly frugivorous diet (Peres 1994; Defler and Defler 1995; Stevenson 2004). However, most of the fruits offered at rescue centers are fruits that are not found in the monkeys' natural diet, and offer energy-rich compounds that are not as useful in the sedentary captive environment. Captive monkeys in reintroduction programs may be unable to recognize natural food items; however, exploration and learning is also possible. For instance, we found an interesting change in food choice over time for the semi-wild group. When they were first sampled in 2011, their diet was mainly made up of new leaves (mostly because they spent a great amount of time feeding on bushes, shrubs, and grass around the station at Base 2). As they became more independent, they managed to exploit different resources in the forest switching their preference to fruits, mainly of the genus *Gustavia,*which was the most common fruiting tree within their home range at that time of the year. They were also observed eating seeds and fruits from a legume tree and experimenting with other fruits from vines. The leaves category, which included all the vegetative parts in plants, still had great importance in their diet (45.1 %), especially *Cyclantaceae* petioles, which became 11.5 % of their food intake. Regarding other food sources, observations during semi-wild1 indicated plasticity in the woolly monkeys' diet: The adult male was observed predating on a frog he had picked up from the forest floor, showing that their diet is not as specialized as previously thought (Defler 2004). M. Gonzalez has mentioned that woolly monkeys in Caparú fed on eggs from a nest, once again showing how much they can vary their diet in order to survive (Gonzalez, pers. comm.) (Fig. 14.11).

We found a low frequency of social interactions in all environments. It is possible that free-ranging animals have enough energy (at least in periods of food abundance) and interest to engage in social interactions. However, captive and released animals have space limitations that may increase the chance of social interactions. Further observations are needed to study in greater detail, the released group's cohesion and social behavior patterns. It is possible that, despite its apparent ecological functionality, the group might not be socially viable. For instance, although sexual solicitation from females was observed, there was no response from the male.

Our results show major differences among the three groups in terms of vertical space usage, and the captive, semi-captive, and wild gradient was once again seen. Cage size is an important limiting variable for captive monkeys because the cages were only 3 m high. However, the monkeys spent most of the time above ground level at high canopy levels, which could be regarded as a positive behavior in terms of predation risk by ground dwellers. Furthermore, during the sampling days, there were some heavy showers that flooded the cages, and this forced the monkeys to climb up to hammocks hanging from the ceiling where they spent their time sleeping, rather than moving around. Perhaps, intentional flooding could be used in captive settings to prevent the use of low strata. Captive monkeys were often seen sleeping on the floor or spending time on the ground manipulating waste and remains from their previous meal. This type of behavior is never observed in wild populations which spend only 2 % of the time at heights below 6 m and never come down to the ground (Stevenson and Quiñones 1993), except in odd situations as, for

Fig. 14.11 Semi-wild2 subadult female feeding on *Gustavia hexapetala,* captive juvenile female feeding on papaya, and semi-wild adult male feeding on a frog on the floor

example, when they accidentally fall from trees. The large amount of time captive individuals spent on the floor was a direct consequence of their enclosure's small size, low complexity, and poor enrichment (Hosey 2005). Being at ground level is not only a risky behavior during the rehabilitation process, as seen for the semi-wild group, but it also represents a great health hazard for captive individuals since it exposes them to sources of disease that they do not normally come in contact with in their natural environment (Epiphanio and Catão-Dias 2003).

Even though during semi-wild1, the group spent most of the time on the ground foraging and feeding on leaves, they also spent a good amount of time foraging for arthropods on floating vegetation (Fig. 14.12). This is an atypical and risky behavior for woolly monkeys. During semi-wild2, even though they frequently used the 0–6 m range, the average height was 9.6 m, closer to the wild preferred height of 12–18 m (Stevenson and Quiñones 1993). During the last sampling days, after the male was rescued, many observations fell into the lower range since, as food was again available at the station at Base 2, monkeys started relying on these resources and spent time on the ground or at ground level. Feeding the animals during this time might have set them back in their process of adapting to the wild environment, but it was a necessary trade-off in order to save and rescue the only adult male from a certain death.

The home range of the semi-wild group was of 350 ha, very similar to the population studied at Caparú Biological Station that ranged between 334 and 440 ha

Fig. 14.12 Semi-wild juvenile and adult females foraging on floating vegetation for arthropods

(Gonzalez and Stevenson 2010), and far greater than the area registered for the population studied at Tinigua National Park (169–200 ha; Stevenson 2006). This result suggests that the released group is investing time and energy exploring the forest for different resources. Woolly monkey home ranges can vary greatly depending on group size and resource availability, showing a negative correlation between forest productivity and home range (Stevenson 2001, 2006).

The overall picture for the rehabilitated and released monkeys (semi-wild) is positive, and the comparison between both sampling periods suggests a progression toward wild behavior, as individuals invested more time on normal activities and learned how to exploit the forest for resources (while they become more independent). There are some big risks associated with the rehabilitation of primates, but these risks might be worth taking in order to accomplish improvements in behavior, such as the ones observed in the released group. Mortality rates at these CAVs (rescue centers) are often high, not only due to captive conditions (poor enclosures, stress, and limited knowledge about arriving individuals) but also because of the health conditions of the individuals on arrival. No official data were provided by the local environmental authority on primate mortality rates at the center, but from conversations with staff members and the case study of the captive group, we estimated a mortality rate of over 60 % for the woollies that have been kept at the center in the past years. The mortality rate at Caparú Biological Station in Vaupés was about the same level or higher for about 15 woolly monkeys that were received there for rehabilitation (Defler, com. pers.). Major causes were health issues and natural predation. During rehabilitation and release processes, the death of subjects is common. At Maikuchiga, we estimate a mortality of around 40 %, from causes varying from preexisting conditions (infections, digestive problems, injuries, etc.), to failure to adapt to the new environment and natural conditions after release. This is a general rule to primate rehabilitation and release, where released animals can suffer from disease and other stress-related problems (Texeira et al. 2007, Richard-Hansen et al. 2000). Each death that occurred during rehabilitation serves as a lesson on ways to improve procedures and provides valuable information to better understand the monkeys' adaptation processes (Fig. 14.13).

Fig. 14.13 Semi-wild adult on the day of his extraction to Base 2 and the same monkey 3 weeks later showing improvement on his health and overall condition

Rehabilitation can be a slow and complicated process of learning and adapting, and it has major risks that have to be taken into account to determine the right and ethical procedures to be followed. The two existing *Lagothrix* subspecies in Colombia face many threats (Botero et al. 2010), and their situation is not improving. Efficient conservation strategies are needed to guarantee the species' survival (Stevenson et al. 2010) not only for its single value as a taxon, but also because of its importance as a key species in maintaining plant diversity in tropical forests (Stevenson 2011). There is abundant evidence on how threatened this species has become due to habitat loss, animal trade, and overhunting, which in turn has resulted in a great number of animals kept in rescue centers and halfway homes, and, in most cases, finally leading to the death of the individuals at these facilities.

Reintroduction through rehabilitation has proven to be functional, but at least in our experience, it is a process involving high mortality rates. Further studies are needed to monitor the destiny of released woolly monkeys and to fully understand the impacts that this process has on the ecosystems where the animals are released. Results from this study suggest that, even though the rehabilitation of woolly monkeys is a slow process and involves many challenges, it is achievable. Rehabilitation therefore appears not only as a promising alternative to the maintenance of animals in rescue centers, which allows animals to have a better quality of life, but, most importantly, it also seems to be an effective conservation strategy for the species in places where they might have been locally extinct or to reinforce dropping populations. Now that we know that rehabilitation is possible, this conservation practice provides a tool for reinforcing or even reintroducing the species to areas where they have become locally extinct. Reintroductions carried out adequately can give this species a fighting chance and help ensure not only its survival but also the maintenance of its important ecological role in plant regeneration processes.

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Chapter 15
Population Viability Analysis of Woolly Monkeys in Western Amazonia

Diego J. Lizcano, Jorge A. Ahumada, Akisato Nishimura and Pablo R. Stevenson

Abstract Colombian woolly monkeys (*Lagothrix lagothricha lugens)* are a critically endangered subspecies with little or no demographic information available to quantitatively assess the impact of various threats (e.g. poaching, disease, and habitat loss) on its population. We use 15 years of published monitoring data on a population of Colombian woolly monkeys in Tinigua National Park, collected between 1987 and 2002, to characterize basic vital rates and population parameters. Our approach uses stage-structured models to estimate population parameters coupled with projections using a state-space model. This coupled approach allows us to take into account population stochasticity and observational uncertainty, the facilitation of incorporation of prior information on population dynamics and on monitoring and simulation processes. Using projection intervals of a year, we found that adult female survival contributes the most to population growth (λ), which is barely increasing for this population (1.009). Hunting of adult females affects population dynamics disproportionately and can lead quickly to population collapse if more than 2 % of females are hunted per year. We also showed that face-whitened disease has a small effect on population growth rate (~ 1 %) but may have a potentially large effect over the long term.

D. J. Lizcano (✉)
Grupo de Investigación en Ecología y Biogeografía (GIEB),
Universidad de Pamplona, Pamplona, Norte de Santander, Colombia
e-mail: dj.lizcano@gmail.com

J. A. Ahumada
Conservation International, 2011 Crystal Drive, Suite 500,
Arlington, 22202, VA, USA
e-mail: j.ahumada@conservation.org

A. Nishimura
Doshisha University, Kyotanabe, Kyoto, 610-0394, Japan

A. Nishimura · P. R. Stevenson
Centro de Investigaciones Ecológicas La Macarena (CIEM),
Universidad de los Andes, Carrera 1 No 18a-10, Bogotá, Colombia

P. R. Stevenson
Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia
e-mail: pstevens@uniandes.edu.co

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Keywords Critically endangered species · *Lagothrix lagothricha lugens* · Neotropical primates · Primate conservation · Stage-structured models · State-space models · Integrated population models

15.1 Introduction

A large proportion of primate species are endangered due to habitat destruction, hunting, and illegal trade, which make their conservation a challenging task (Chapman and Peres 2001). Although it has been argued that no species has gone extinct due to recent anthropogenic disturbance until the end of the twentieth century (Wright and Jernvall 1999), the tropical and subtropical habitats where they live have been shrinking, and about half of the taxa (47.8 % of 634) are currently recognized as having some risk of extinction (Schipper et al. 2008). Extinction risk has been usually associated with rarity, which in turn has been attributed to low population density, small geographic ranges, and narrow ecological niches (Fagan and Holmes 2006; Holmes and Fagan 2002).

Conserving endangered species is a difficult task that should be supported by scientific knowledge. For some of the most endangered primates, there is a lack of basic ecological information, such as geographic range and population density (Mittermeier et al. 2009). However, a proper evaluation of the chance of extinction needs data on population size, spatial distribution, threats within the geographic range, and, ideally, information on population dynamics, behavior, and genetic traits (Chaves et al. 2011; Strier et al. 2006; Strier and Ives 2012). To assess the growth of a population based on demographic parameters, it is important to include some level of uncertainty. Demographic uncertainty should be considered, since birth and death rates, as well as survival and fecundity, might be affected by changes in resource abundance, predation, or climate change (Dunham et al. 2010; Gregory et al. 2012; Palacios and Peres 2005; Wright and Jernvall 1999). For instance, populations of howler monkeys are known to vary drastically in their density, possibly due to the influence of diseases such as yellow fever (Rudran and Fernandez-Duque 2003). However, knowledge of population dynamics and potential causes of variation on natural populations must rely on long-term field studies.

Colombian woolly monkeys (*Lagothrix lagothricha lugens,* sensu Fooden 1963 and supported by Botero et al. 2010) have been categorized as critically endangered (Stevenson and Link 2008). They live in sub-Andean and lowland forests along the central and eastern ridges of the Colombian Andes. This region, including the northern Atlantic plains, corresponds to the areas with the highest human populations and deforestation rates in the country (Armenteras et al. 2011; Etter et al. 2008). The first field studies of this taxon were conducted in the 1970s with ecological observations on one population in northern Colombia (Kavanagh and Dresdale 1975). At the same time, Japanese researchers in the Caquetá region described the social and ecological aspects of the species as living in large groups and feeding mostly on ripe fruits (Izawa 1976; Nishimura 1990). In the 1980s, the same group of researchers established a new field site for the study of primates near La Macarena Mountains (Meta), in collaboration with Universidad de Los Andes (Nishimura et al. 1996). Currently, our knowledge of the ecology and behavior of Colombian woolly monkeys comes from this site which nowadays is part of Tinigua National Park. This population is recognized for its efficient role as seed dispersers (Stevenson 2000), in part, due to the quantitative component of seed dispersal, which is directly proportional to the high population density (41–50 ind.km^{-2}; Stevenson 2007). The high population density of woolly monkeys at Tinigua National Park is uncommon, given that they are one of the largest primate species in the community (along with spider monkeys) and it is uncommon for large primates to have high densities (Reed 1999). In spite of this, there is evidence of population growth in several groups of woolly monkeys over time at Tinigua (Nishimura 2003; Stevenson 2007; Stevenson and Castellanos 2000). Unfortunately, due to the presence of armed guerilla groups in the area, it has been impossible to continue studying this population since 2002. Other populations in Colombia—such as the one in Serranía de San Lucas—have been difficult to relocate due to security problems, and populations in Caquetá are under severe deforestation pressures. Currently, there is only one population of free-ranging Colombian woolly monkeys under study in Cueva de los Guacharos National Park, which has been followed since 2009 (Vargas et al. 2014). However, demographic data for this population are still unavailable, limiting availability of demographic records to about 15 years of information collected by Nishimura (2003) in Tinigua Park.

Our aim in this study is to analyze the demographic trends of the population at Tinigua National Park, based on 15 years of observations of a single group. In addition, we compared population trends given different scenarios of disease prevalence and hunting pressure. Since there are no studies of population viability published for this species, we hope that the information presented here may be valuable for conservation purposes.

15.2 Methods

The group composition of woolly monkeys was recorded yearly from 1987 to 2002 by visual census in Tinigua National Park, Colombia. Details of census methods are found in Nishimura (2003). The individuals were classified as infants (0–1 year old), juveniles (>1–4 years old), subadults (>5–6 years old) and adults (>6 years old). Aspects of the population dynamics such as population size, natality, and survival were investigated with matrix population models (Caswell 1989), with the aid of the R software (R Core Team 2012) and the packages popbio (Stubben and Milligan 2007) and JAGS (Plummer 2003). The complete stage-classified life cycle graph of woolly monkeys in Tinigua Park is given in Fig. 15.1. During a projection time interval, an individual in stage k may survive and grow to stage $k+1$ with probability Gm_k for males and Gf_k for females, and may survive and remain in stage

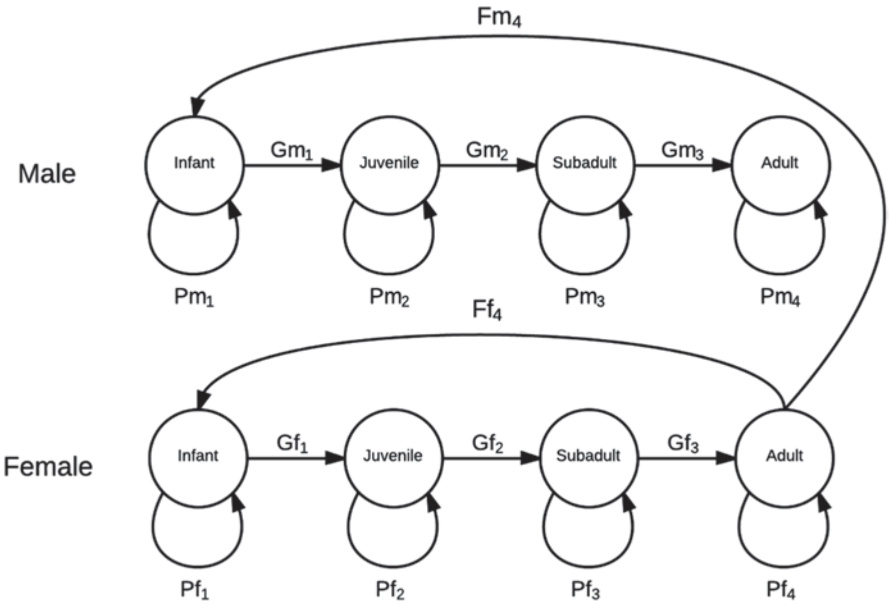

Fig. 15.1 Complete stage-classified life cycle graph of Colombian woolly monkeys (*Lagothrix lagothricha lugens)*. *Gm* and *Gf* are survival and growth to next age probabilities for males and females, respectively. *Pm* and *Pf* are probabilities of survival and remaining in the same age for males and females. *Fm* is fecundity of females

k with probability Pm_k and Pf_k for males and females, respectively. Females reproduce, with fertility F, producing new individual males or females (Fm_k or Ff_k) in the smallest class (infant). We used projection intervals of a year in this study.

To calculate a transition matrix based on the census data, we implemented the Wood's quadratic programming method (Caswell 1989; Wood 1997) on the intervals Δt_i on time series from 1987 to 2002, making 15 group composition vectors $\mathbf{n}i(t) = [n_{i1}(t) n_{i2}(t) n_{i3}(t) n_{i4}(t)]^T$, where $n_{ik}(t)$ is the number of individuals of stage k at time t of interval Δt_i, $t = 1,\ldots,15$, and superscript T denotes the transposition of vector $\mathbf{n}i(t)$. The 15 intervals represent 1 year each.

The matrix representing females is

$$\begin{aligned}
n_{i1}(t+1) &= Pf_{i1} x\ n_{i1}(t) + N_{i1} \\
n_{i2}(t+1) &= Gf_{i1} x\ n_{i1}(t) + Pf_{i2} x\ n_{i2}(t) \\
n_{i3}(t+1) &= Gf_{i2} x\ n_{i2}(t) + Pf_{i3} x\ n_{i3}(t) \\
n_{i4}(t+1) &= Gf_{i3} x\ n_{i3}(t) + Pf_{i4} x\ n_{i4}(t) \quad \text{with } t = 1,\ldots,15
\end{aligned}$$

which can be expressed in matrix form as the equation

$$n_i(t+1) = K_i(t+1) \cdot p_i \tag{1.1}$$

where

$$p_i = (Pf_{i1}\; Gf_{i1}\; Pf_{i2}\; Gf_{i2}\; Pf_{i3}\; Gf_{i3}\; Pf_{i4}\; Gf_{i4})^T \tag{1.2}$$

and $K_i(t)$ is the matrix

$$\begin{bmatrix} n_{i1}(t) & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & n_{i1}(t) & n_{i2}(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & n_{i2}(t) & n_{i3}(t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & n_{i3}(t) & n_{i4}(t) & 0 \end{bmatrix}$$

By defining the vector z_i and the matrix M_i as the observed quantities, then for each interval Δt_i we have

$$z_i = M_i \cdot p_i \tag{1.3}$$

To estimate the parameters in p_i, the sum of squared deviations between z_i and $M_i p_i$ should be minimized:

$$\text{minimize} \left\| z_i = M_i \cdot p_i \right\|^2 \tag{1.4}$$

which according to Caswell (1989) is equivalent to

$$\begin{aligned} &\text{minimize}((p_i^T \cdot G_i \cdot p_i)/2 + f_i^T \cdot p_i) \\ &\text{where}\, G_i = M_i^T \cdot M_i \;\; and \;\; f_i = -M_i^T \cdot z_i \end{aligned} \tag{1.5}$$

However, parameters P_k, G_k, and N_1 should be nonnegative, and P_k and G_k represent independent probabilities of the fate of an individual in stage k, so that their sum cannot exceed 1 (i.e., $P_k + G_k \le 1$, $k = 1, 2, 3$, and $P_4 \le 1$). These constraints are expressed in matrix form as

$$C \cdot p_i \le b \tag{1.6}$$

Therefore, the complete specification of the quadratic programming problem is

$$\begin{cases} minimize\left(\dfrac{p_i^T \cdot G_i \cdot p_i}{2} + f_i^T \cdot p_i \right) \\ \qquad subject\, to\; C \cdot p_i \le b \end{cases} \tag{1.7}$$

This problem was solved using *R,* with the function "QPmat" from the package popbio (Stubben and Milligan 2007), which is an implementation in *R* of the MATLAB "qp" routine, originally developed by Caswell (1989). By solving the quadratic programming problem for all Δt_i subsequently, we obtained the transition matrix for females and males as follows:

$$T_i = \begin{bmatrix} Pf_1 & 0 & 0 & Ff_4 & 0 & 0 & 0 & 0 \\ Gf_1 & Pf_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & Gf_2 & Pf_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & Gf_3 & Pf_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & Fm_4 & Pm_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & Gm_1 & Pm_2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & Gm_{20} & Pm_3 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & Gm_3 & Pm_4 \end{bmatrix}$$

We used the transition matrix to develop a projection model as a linear, time-variant system of differential equations, expressed in matrix form as

$$n(i+1) = T_i \cdot n(i) + \left[N_{i1} 0\ 0\ 0\ 0\ 0\ 0\ 0\right]^T \tag{1.8}$$

Taking into account that the probability of death for stage k during a projection interval at time *i,* is defined as m_{ik} and is equal to

$$m_{ik} = 1 - \sum\nolimits_n t^i_{\mathrm{nk}} \tag{1.9}$$

From the projection model, we calculated the dominant eigenvalue or lambda (λ) and performed sensitivity and elasticity analyses (Caswell 1989). Sensitivity analysis is useful to evaluate how an absolute change in a vital rate affects λ, i.e., it allows determining the influence of the vital rates on the population dynamics. Sensitivity value is calculated as the slope of the line between λ and a vital rate. Elasticity analysis is used to estimate the effect of a proportional change in the vital rates on population growth. In essence, elasticities are proportional sensitivities, scaled so that they are dimensionless, which allows for direct comparisons of survival and reproductive matrix elements.

Simulations of Hunting We performed population-growth simulations under a hunting scenario, varying the probability of female survival in the projection matrix and then recalculating λ for the population. Female survival ranged from the initial estimated value of survival probability (~0.99) down to 0.4 in 0.1 intervals. The effect of hunting was calculated as the new population growth rate λ_{i} divided by the starting value of lambda.

Impact of Face-Whitened Disease To evaluate the impact of face-whitened disease on the population (Nishimura 1999), we developed a state-space model, which included a set of process equations describing the true but unknown development of the states (i.e., population sizes) across time and a set of observation equations linking the true states with the data (i.e., population counts). The process equations are a Markovian process where population size in year $t+1$ depends on population size in year t (Buckland et al. 2004; Kéry and Schaub 2011). These equations described population size as a function of demographic rate (λ) and initial population size. For the observations which were conditioning for the process, we assumed that the population count in year t (y_t) consisted of the number of individuals estimated as

$$y_t = (N_0 \lambda^t) + \varepsilon \tag{1.10}$$

where we assumed that in each year t, an observational error ε was made while counting individuals. Thus, the observed time series of counts can be decomposed in a process variation and an observation error component. The latter was assumed to fit a normal distribution with mean zero and variance σ_y^2 and is in fact a residual error that incorporates the observation error of counts and the lack of fit of the state equations to the true (but unobserved) dynamics of the population under study (Kéry and Schaub 2011). For this model, priors were specified for mean growth rate as the value of λ obtained from the matrix population model and for initial population size as ten individuals. A first model was specified in JAGS (Plummer 2003) using three chains with 200,000 draws, 6 as thinning rate, and 10,000 burning length. A second model was specified using a different prior for mean growth rate, which corresponded to the value of λ in the matrix population model, assuming none of the individuals died of the disease. In the census data, four females and two males were found dead due to face-whitened disease.

15.3 Results

Based on the estimated projection matrix, survival probability was highest for adult females (0.934) and slightly lower for adult males (0.865). Female fertility was slightly higher for infant females (0.237) than for infant males (0.204; Table 15.1). The dominant eigenvalue (λ) estimated for the woolly monkey population was 1.009, indicating that the population has a potential to grow, although very slowly. Projecting the transition matrix through time, starting with no male infants and two individuals in the other stages, showed that the adult female stage increased faster than any other stage. Male infants and female subadults did not increase, but steadily decreased in the 1st year and stabilized after the 5th year (Fig. 15.2).

Based on the sensitivity analysis, adult female survival and the transition probability from juvenile to subadult females have the highest impact on λ (Table 15.2). Inspection of the elasticity matrix shows that, by far, survival of adult females is the most important matrix element in terms of λ. The elasticity for adult female survival was 0.611, which indicates that 1 % increase in female adult survival will cause 0.611 % increase in λ. The transition probability from subadult to adult females was the second most influential element on λ (Table 15.3).

Table 15.1 Woolly monkeys' projection matrix

	Female infant	Female juvenile	Female subadult	Female adult	Male infant	Male juvenile	Male subadult	Male adult
Female infant	0.258	0	0	0.237	0	0	0	0
Female juvenile	0.518	0.613	0	0	0	0	0	0
Female subadult	0	0.188	0.677	0	0	0	0	0
Female adult	0	0	0.323	0.934	0	0	0	0
Male infant	0	0	0	0.204	0.205	0	0	0
Male juvenile	0	0	0	0	0.323	0.73	0	0
Male subadult	0	0	0	0	0	0.27	0.724	0
Male adult	0	0	0	0	0	0	0.244	0.865

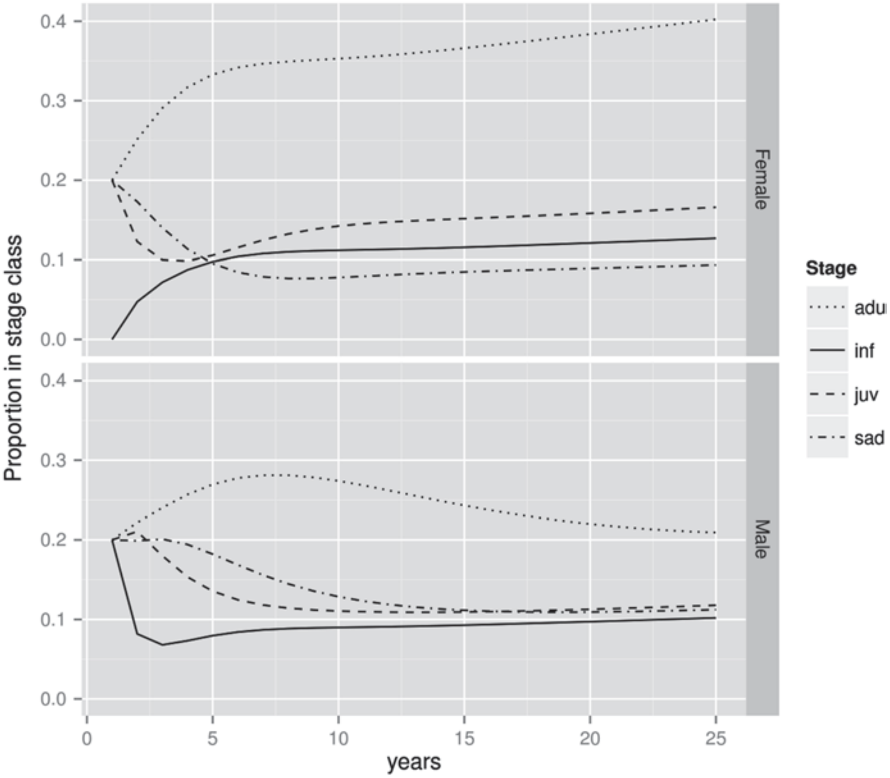

Fig. 15.2 Population projection to 25 years for each woolly monkey age stage discriminated by sex. All stages start in two individuals except female infant which started in cero. The time step used was one year

Table 15.2 Woolly monkeys' sensitivity analysis

	Female infant	Female juvenile	Female subadult	Female adult	Male infant	Male juvenile	Male subadult	Male adult
Female infant	0.066	0	0	0.209	0	0	0	0
Female juvenile	0.096	0.125	0	0	0	0	0	0
Female subadult	0	0.264	0.149	0	0	0	0	0
Female adult	0	0	0.153	0.66	0	0	0	0
Male infant	0	0	0	0	0	0	0	0
Male juvenile	0	0	0	0	0	0	0	0
Male subadult	0	0	0	0	0	0	0	0
Male adult	0	0	0	0	0	0	0	0

Table 15.3 Woolly monkeys' elasticity analysis

	Female infant	Female juvenile	Female subadult	Female adult	Male infant	Male juvenile	Male subadult	Male adult
Female infant	0.017	0	0	0.049	0	0	0	0
Female juvenile	0.049	0.076	0	0	0	0	0	0
Female subadult	0	0.049	0.1	0	0	0	0	0
Female adult	0	0	0.049	0.611	0	0	0	0
Male infant	0	0	0	0	0	0	0	0
Male juvenile	0	0	0	0	0	0	0	0
Male subadult	0	0	0	0	0	0	0	0
Male adult	0	0	0	0	0	0	0	0

Simulations of adult female hunting showed that a small harvest of two females per year per 100 females can tip the value of λ below 1, thus leading to a decrease in population size (Fig. 15.3). Hunting one adult female per year would result in a reduction of λ, so that the population would still grow, but at a slower rate.

Estimated projections of the census data using a state-space model reveal a slow growth rate with group size dropping in 1992. After that year, the group recovered, showing a peak in group size by the year 1997, when the population started a slow decrease. Projections of the model after the last census year show a slow but steady increment in estimated group size (Fig. 15.4a). The probability of ending with a larger group size in 2013 compared to the last observed group size in 2002, $N(2013) > N(2002)$, was 0.52.

Estimated projections of the census data with "artificially" extended life of individuals that died by face-whitened disease resulted in a calculated λ of 1.018, which is an increase in 0.9 % compared to the original λ (1.009) with disease mortality included. Fluctuations were also less marked, including the 1992 drop, which would have a very low impact on estimated group size. Projections of the second model after the last census in 2003 show a continuous increase in the group size (Fig. 15.4b). The probability of ending with a larger group size in 2013 compared to the last observed group size in 2002, $N(2013) > N(2002)$, was 0.738 (an increase of 40 % compared to the simulations with disease). The difference in estimated growth rate between the population that suffered from face-whitened disease and the population

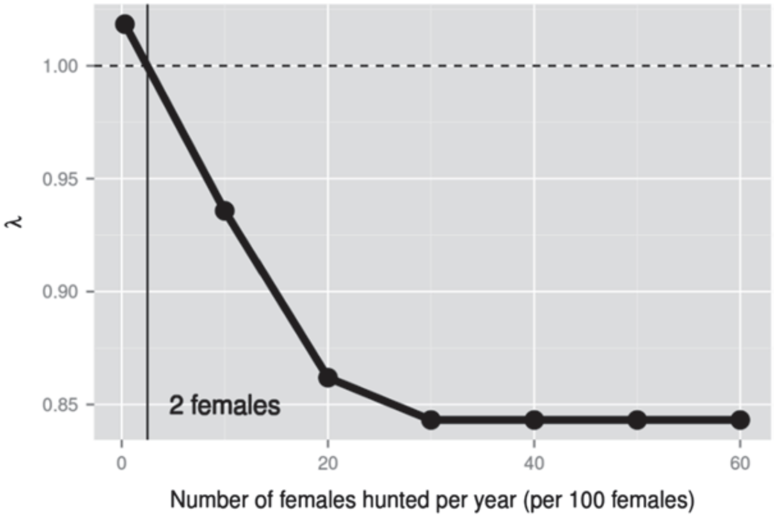

Fig. 15.3 Effect of hunting intensity on λ for a hypothetical population of 100 females

that did not is not very large (~ 1 %), but demographically speaking, this difference in λ would result in the disease-free population having 54 % more individuals than a disease-laden population after 50 years of growth. This suggests that this disease may have an important impact on the dynamics of the population.

15.4 Discussion

A general consensus in population dynamics studies suggests that changes to the demographic rates of older or larger individuals have less impact on population growth than do equivalent changes among younger or smaller individuals. However, the generalization of these rules depends in each case on the biology of each species, delimitation of age stages, and results of sensitivity and elasticity analyses (Carslake et al. 2009). In our particular case for this population of woolly monkeys, the population parameter that contributed the most to population growth is adult female survival. Several population growth studies in primates have found similar patterns, where survival and fecundity of adult females are the most important factors determining the population growth: muriqui monkeys (Strier 1993), howler monkeys (Mandujano and Escobedo-Morales 2008), baboons (Alberts and Altmann 2003), and tarsiers (Neri-Arboleda 2010). Another study with ateline monkeys (*Brachyteles*) has also found a relevant role of female fertility on population growth and differences in mortality rates between age and sex classes (Strier and Ives 2012). In particular, the population of *Brachyteles* showed a large increase from 60 to nearly 300 individuals during a period of 28 years, which was presumably

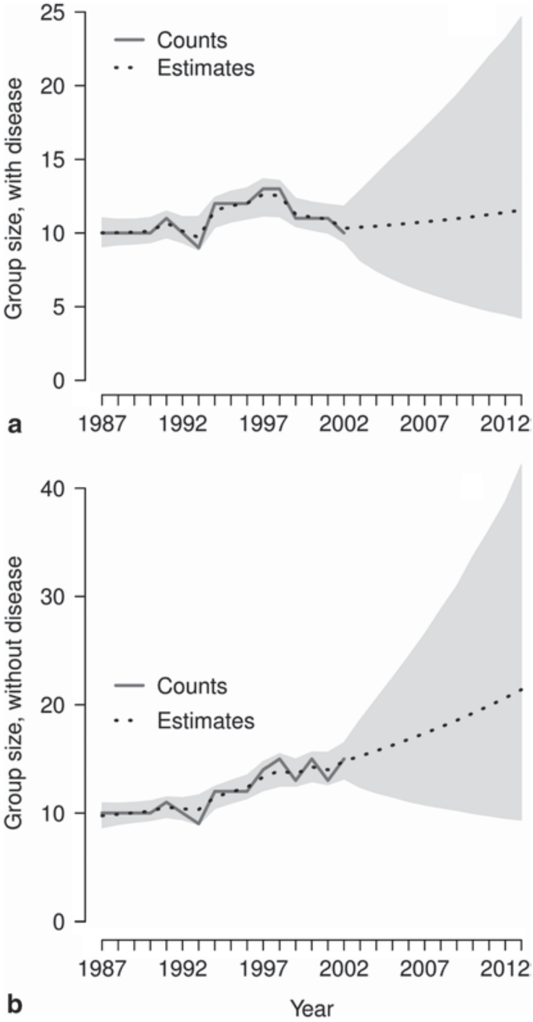

Fig. 15.4 Population projection using state space models comparing the population with face-whitened disease (**a**) and without it (**b**). The simulation for *panel b*, included artificial extension of the life of woolly monkeys that died from the disease in *panel a*. *Gray areas* indicate variation coefficient of 95 %

due to an expansion of used habitat (resources on the ground were included in the diet). The transition probability from juvenile to subadult females in our study also showed high λ sensitivity but to a lesser degree than the *Brachyteles* (Table 15.2). This pattern could be related to the observations of frequently dispersing subadult female woolly monkeys (Di Fiore et al. 2009; Di Fiore and Fleischer 2005). Survival and transition rates in other stages were not as sensitive to changes in λ.

Our woolly monkey study group showed a slow increase in size since 1987 despite the constraints imposed by the disease. We cannot ascertain whether this is due to the face-whitened disease, or some other mechanism such as intraspecific or interspecific competition for fruit, or environmental and demographic stochasticty, which were not explicitly considered in our study. Small differences in resource use, in terms of food and habitat use, play an important role in resource partitioning between primates at the study site (Stevenson et al. 2000), potentially affecting the vital rates of woolly monkeys. As large frugivores, woolly monkeys need large areas of continuous forest as a prerequisite to meet their food requirements (Stevenson 2006). However, deforestation in some regions of the Colombian Amazon has increased in the past 10 years (Armenteras et al. 2006; Armenteras and Retana 2012; Sánchez-Cuervo et al. 2012), increasing the vulnerability of woolly monkey populations to hunting (Alvard et al. 1997; Peres and Palacios 2007) and environmental stochasticity (Saccheri and Hanski 2006). Simulations of population growth without the disease (essentially, letting the diseased individuals live in the model) showed a modest (~1 %) increase in population growth, that could, however, compound with time, account for 54 % difference in the number of individuals after 50 years.

The simulated effect of hunting on woolly monkeys highlights how sensitive they are to harvesting (Fig. 15.3). Exceeding a harvest rate of 2 % of the females in a group may cause a precipitous drop in the growth rate of the population, bringing it below 1 and therefore causing a population decline. Hunting practices of primates by indigenous people and settlers in the Amazon often target females with infants, to keep the infants as pets (Defler 2010). This practice affects the population dynamics of this species, since it targets the stage that contributes mostly to population growth.

Hunting of large primates such as woolly monkeys can cascade down the food chain and affect other vertebrate species and even the dynamics of plant communities (Harrison et al. 2013; Peres and Palacios 2007; Terborgh et al. 2008; Stevenson 2011). Disappearance of large vertebrates from tropical forests has been identified as a potential trigger of large changes in the spatial seed rain (Bueno et al. 2013; Hansen and Galetti 2009). One consequence of their extinction is change in forest diversity due to negative effects on the recruitment of several plant species, particularly those with large seeds dispersed by woolly monkeys (Stevenson et al. 2005).

We can conclude from this analysis that the population of Colombian woolly monkeys is experiencing very slow growth-rate dynamics, which suggests that several mechanisms might be in place (e.g., slow reproductive rates and potential biotic interactions such as competition, disease, or predation). From this analysis, we estimated the effect of only one disease, the face-whitened disease (Nishimura 1999). Our analysis suggests that the disease has a small impact (decrease of 1 %) on the population growth rate of the species, but even such a small difference in λ can have a large compound effect over the years, 54 % increase in the number of individuals after 50 years. Woolly monkeys are known to harbor many other diseases, including malaria, hepatitis, toxoplasma, and yellow fever (Bouer et al. 1999; Gyimesi et al. 2006; Kozakiewicz et al. 1999; Lanford et al. 2003). We can hypothesize that diseases may play an important role in maintaining population size through time.

Our analysis of hunting shows that this population must not be harvested above 2 % of the female population per year. The Tinigua population might be atypical in size, with one of the highest densities ever reported (Stevenson 2007), which might be more susceptible to competition and disease transmission than to low levels of hunting. However, it is clear that medium and high levels of hunting can strongly decrease population density of large primates such as spider and woolly monkeys (Peres and Palacios 2007).

This paper highlights the importance of monitoring and collecting long-term demographic information on primates which is essential to proper and informed conservation and management practices, particularly for species that are endangered. We hope that field primatologists continue to collect long-term data, particularly for threatened species, in order to assess the viability of other populations. These data, coupled with novel integrated population models and Bayesian inference, will provide more precise information, to make better decisions on population dynamics, e.g. under climate-change scenarios. It is clear that the survival of this species requires low probability of local extinction in several locations (Brito et al. 2008), which seems a huge challenge as habitat destruction and hunting continues throughout the range of Colombian woolly monkeys (Armenteras et al. 2011; Sánchez-Cuervo et al. 2012; Stevenson and Link 2008).

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Chapter 16
Yellow-Tailed Woolly Monkey (*Lagothrix flavicauda*): Conservation Status, Anthropogenic Threats, and Conservation Initiatives

Noga Shanee and Sam Shanee

Abstract This chapter examines threats and conservation opportunities for the Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*), a species endemic to northeastern Peru. Inherent traits make this species susceptible to extinction from threats identified here as habitat loss, hunting, selective logging, road construction, extractive industry, and climate change, all of which are increasing. Using current range estimates, available habitat, and published density estimates, we present here the first estimate for *L. flavicauda* population size. We estimate a current population of between 88,622 and 10,564 individuals, which represents a reduction of between 46 and 93 % of the estimated original population since 1981. These numbers represent maximum population estimates as they only consider habitat availability, disregarding hunting pressure. It is clear that both the species' population size and habitat are decreasing. State conservation efforts do not fully mitigate threats to this species, but land protection by private actors, especially rural communities through the creation of protected areas and landscape-level conservation, offers an innovative and increasingly popular conservation alternative.

Keywords *Lagothrix flavicauda* · Yellow-tailed woolly monkey · Conservation status

16.1 Introduction

The yellow-tailed woolly monkey is one of the largest and rarest neotropical primates, and it is the largest mammal endemic to Peru. It has been listed as Critically Endangered since 1996, categorized as A4c (www.iucnredlist.org), and has fea-

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N. Shanee (✉) · S. Shanee
Neotropical Primate Conservation, 23 Portland Road,
Manchester, M32 0PH, UK
e-mail: nogashanee@gmail.com

S. Shanee
e-mail: samshanee@gmail.com

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tured four times, since the year 2000, on the list of the World's 25 Most Endangered Primate Species by the International Primatological Society (Mittermeier et al. 2012). *Lagothrix flavicauda* is also categorized as Endangered under Peruvian law (D.S. 034–2004-AG).

L. flavicauda is restricted to a small area of cloud forest between 1,400 and 2,700 m in the departments of San Martin and Amazonas, and in small areas of Huánuco, and La Libertad (DeLuycker 2007; Shanee et al. 2007a, 2008b; Leo Luna 1980, 1982, 1989; Shanee 2011; Buckingham and Shanee 2009). Their distribution area is located in the heart of the Tropical Andes Biodiversity Hotspot in northeastern Peru, the most biologically diverse region on earth, and also one of the most threatened (Mittermeier et al. 2004). Many of the anthropogenic pressures faced by *L. flavicauda* are unique to its small range within this hotspot. The main threats for the yellow-tailed woolly monkey are the continued growth of human populations and associated habitat destruction and hunting (DeLuycker 2007; Shanee et al. 2007a, 2008b; Leo Luna 1980, 1982; Shanee 2011).

Many of the predictors of the species' extinction risk, such as small and decreasing population size (O'Grady et al. 2004), small geographical range size and slow life histories (Purvis et al. 2000), complex social structure (Courchamp et al. 1999), and conspicuous behaviors which can lead to increased hunting (Soule 1983) are present in *L. flavicauda*. Harcourt et al. (2002) identified high resource use (defined as a combination of large body mass, large annual range, and high local density and group size), low reproductive rates, and habitat or dietary specialization as the main factors defining a species' intrinsic risk of extinction, again traits shown by *L. flavicauda*.

In this study, we calculate estimated population size and trends for *L. flavicauda,* and we identify the main threats for the species, in the context of its intrinsic predisposal to extinction. We also look at conservation initiatives in northeastern Peru and their potential for conserving this species.

16.1.1 Restricted Range and Habitat Preference

L. flavicauda's habitat is characterized by rugged terrain consisting of steep mountainsides and deep river gorges. Shanee (2011) suggests that this species is predominately found in *Ficus* spp., dominated by pre-montane and montane cloud forests. Habitat quality varies greatly among different elevations and soil compositions, which probably leads to differences in home range size and population densities within the species' distribution (as shown for other ateline species: Palacios and Peres 2005; Shanee 2009). Shanee and Shanee (2011) found that *L. flavicauda* is able to survive at relatively high densities, at least in the short term, where forest disturbance is high.

The reported diet of *L. flavicauda* includes leaves, lichen, epiphytes, bromeliads, buds, and ripe fruits, with *Cecropia* spp. and *Ficus* spp. as the most important genera in the diet of these primates (Cornejo 2007; Leo Luna 1980; Shanee and

Shanee 2011; Shanee, this volume). This species appears to be more folivorous than other woolly monkey species and spider monkeys (Shanee, this volume). This reduction in fruit consumption and higher reliance on non-fruit plant matter with increased elevations agree with documented variations in the diet of other frugivorous primates between low and high elevations (Hanya et al. 2003; Sayers and Norconk 2008). As suggested by Shanee (this volume), this lower consumption of ripe fruit lessens the need for large home ranges especially in times of reduced fruit production. This provides an additional explanation for the species' ability to survive in disturbed or less productive habitat and presents opportunities for the species' conservation in anthropogenic landscapes.

In 1981, it was estimated that the area of forested habitat suitable for the species was of at least 11,240 km², and that by 1991 the available forest would be reduced to 9,500 km² (Leo Luna 1982). In 2007, DeLuycker and Heymann calculated deforestation rates and estimated that by 2006 the potential forested habitat would be reduced to 7,240 km². The most complete evaluation (Buckingham and Shanee 2009) estimated that the remaining habitat was of 6,302 km². These estimates were based on information on the remaining habitat in the departments of Amazonas and San Martin, which, however, did not take into account the forested habitat in the neighboring departments of Huanuco and La Libertad (Shanee 2011). We adjusted the results of Buckingham and Shanee (2009) to include additional areas where *L. flavicauda* has been found (Shanee 2011). Maps were constructed using ArcGIS software (ESRI 2011) based on the geographic data acquired from governmental agencies and NGOs working in the area.

Using the same criteria as Buckingham and Shanee (2009), the additional habitat area was estimated to be 552.9 km², of which only 177.6 km² were considered as suitable habitat. Thus, the total original range estimate was of just under 12,000 km², and the current range is between 6,854 and 2,201 km². This small range size indicates a high natural tendency to extinction (Purvis et al. 2000). Contrastingly, the distributions of most other ateline primates cover much wider areas, which usually include several countries and habitat types (Groves 2001; Di Fiore et al. 2011). Larger distributions reduce vulnerability not only to biological risks of extinction but also to anthropogenic threats related to sociopolitical situations.

Using the above range estimates and published density estimates (Table 16.1), we estimate that the original maximum population of *L. flavicauda* was just more than 155,000 individuals. Based on current estimates of available habitat, we place the maximum extant population of *L. flavicauda* between 88,622 and 10,564 individuals. This represents a reduction between 46 and 93 % of the original population, with an average of 62,522 individuals, which represents a reduction of around 60 % since 1981. We present these as estimates of maximum population size since they only take into account habitat availability and do not consider the effect of commercial and subsistence hunting, a serious threat to this species.

Table 16.1 Comparative individual and group density estimates for *L. flavicauda*

Source	Study site	Elevation (masl)	Individual densities (per km²)	Group density (per km²)	Method
Shanee (this volume)	La Esperanza, Amazonas	2,000	8.8[a]	0.82[b]	Minimum convex polygons
Shanee (this volume)	La Esperanza, Amazonas	2,000	4.8[a]	0.45[b]	Kernel density analysis
Shanee and Shanee 2011	La Esperanza, Amazonas	2,000	9.26	1.04	Transect width estimation
Shanee and Shanee 2011	La Esperanza, Amazonas	2,000	8.27	0.93	Krebs (1999)
Shanee and Shanee 2011	La Esperanza, Amazonas	2,000	10.32[c]	1.16	Ad-lib group count
Leo Luna 1982, 1987	Rio Abiseo National Park, San Martin	–	2.25–9[d]	0.25–1	Line transect
Cornejo 2007	Abra Patricia Private Conservation Area, Amazonas	2,100	5.14–12.93	0.93–2.24	Line transect
Max	–	–	12.93	2.24	–
Min	–	–	4.8	0.45	–
Average	–	–	7.86	0.98	–

[a] Calculated from average group size of 10.7 (Shanee, this volume)

[b] Taken from 95% minimum convex polygon (MCP) and kernel density estimation (KDE) estimates (Shanee, this volume)

[c] Calculated from average group size of 8.9 (Shanee and Shanee 2011)

[d] Calculated from average group size of 9 (Leo Luna 1982, 1987)

16.1.2 Anthropogenic Threats to L. flavicauda

Deforestation

A species-intrinsic predisposal to extinction, especially in disturbed habitats, is suggested to be related to body size, ecological specialization, geographic distribution, population density or rarity, and dietary specialization, among others (Johns and Skorupa 1987; Brashares 2003; Cardillo et al. 2005; Kotiaho et al. 2005; Purvis et al. 2000). Although *L. flavicauda* populations do persist where forest disturbance is high (Shanee 2011; Shanee and Shanee 2011), the species' ecology and natural history would suggest a greater sensitivity to deforestation and fragmentation.

According to Peruvian government publications, by the year 2000, Peru had lost 7,172,953 ha of its original forest cover. The regions with the highest deforestation rates are the following: San Martin with 1,327,736 ha, equivalent to 25.9% of its total area and Amazonas with 1,001,540 ha, equivalent to 25.5% of its total area cleared (PROCLIM/CONAM 2005). The San Martin Regional Government reports that deforestation in the region started around the 1940s, following the government colonization policies of the time, at a rate of 8,000 ha per year. In the 1960–1970s, deforestation escalated to 55,000 ha per year. The most recent data available, from

1989 to 2002, show a rate of 11,000 ha cleared annually.[1] No official estimates for the Amazonas region exist.

Deforestation usually follows a pattern starting with small patches of non-forested areas, generally in low and flat lands, which expand over time reaching higher lands and steep slopes. Farmers clear surrounding areas resulting in thinning corridors between fields. With time, corridors are reduced to a line of trees, and forest clearing moves further into less accessible areas. *L. flavicauda* uses these corridors to move between forest patches (Shanee and Shanee 2011). It has been reported that when there is complete discontinuity/isolation, *L. flavicauda* can descend to the ground to cross short distances between forest patches (Shanee et al. 2007b). However, this behavior increases predation risks (Di Fiore 2002). Also, the carrying capacity of forest patches can be exceeded resulting in population crash or a reduction in population numbers due to selective pressures (Cowlishaw and Dunbar 2000). Moreover, many *L. flavicauda* populations survive in totally isolated forest fragments (Shanee et al. 2007a; Shanee 2011), thus increasing the risk of genetic drift through inbreeding (Frankham 1995).

As in many other regions, cattle ranching is the main cause of deforestation and habitat loss throughout the *L. flavicauda* distribution range (Steinfeld et al. 2006). Erosion on steep slopes and low economic investment in improving ranching methods result in a very low cattle to area ratio (approximately 1–2 head per ha). According to Shanee (2012a), monopoly companies dramatically increase the destruction of *L. flavicauda* habitat due to the demand for increased dairy production, without promoting or supporting sustainable practices. Exploitative companies and unsupervised intermediaries discriminate small-scale production and, by doing so, force the maximization of production by further unsustainable methods (Shanee 2012a). The farming of coca crops (*Erythroxylum coca*) and the environmental and social effects of persistent actions against it are also an essential cause of cloud forest destruction in the south of San Martin and Huánuco (Fjeldså et al. 2005; Young 1996).

Human population growth throughout *L. flavicauda's* range is among the highest in Peru (INEI 2007). Migrants arrive mainly from the mountain regions of Cajamarca, where mining concessions currently occupy almost 50 % of the area (calculated from: MEM 2011), resulting in increasing land prices, social instability, and a lack of drinking water and fertile land. Also, the proliferation of large-scale palm oil and rice production in the eastern lowlands forces many small farmers to migrate higher up to new areas (Shanee 2011). Migrants are usually impoverished and are forced to invade forested lands, which are then transformed using unsuitable farming methods (Bebbington 1990; Shanee 2012a).

Land tenure in rural Peru is largely unregulated and land trafficking is common in the cloud forest. Studies from Latin America show that informal land tenure promotes deforestation (Southgate et al. 1991; Pichón 1997), reduces the value of forested land, and encourages conversion of forest to pasture (Araujo et al. 2009). Also, in areas where property rights are claimed through forest clearance, as is

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[1] Reátegui García, regional director of Natural Resources and Environmental Management, at the Regional Forum on Forest Politics and Climate Change in Tarapoto, June 2010.

the case in northeastern Peru, land titling projects encourage further deforestation (Kaimowitz 1996; Mendelsohn 1994).

Hunting

Studies have shown that *L. flavicauda* populations are also threatened by hunting activities (Shanee et al. 2007a, 2008a; Leo Luna 1987; Shanee 2012b). Due to their low reproductive rates and population densities, large-bodied primates are particularly vulnerable to hunting, which can result in local extinctions (Jerozolimski and Peres 2003; Peres 2001; Robinson and Bennett 2000; Bodmer et al. 1997). Bush meat consumption is considered the greatest threat to primates in Central and South America (Peres 2001), as primates present a significant part of bush meat extracted from tropical forests (Robinson and Bennett 2004; Robinson and Bodmer 1999). For a Critically Endangered species, such as *L. flavicauda,* even low levels of local hunting could be disastrous. *L. flavicauda'*s inherent curiosity and conspicuous nature make it particularly easy to hunt.

Wildlife trafficking generally follows the main highway from the lowlands of Loreto and San Martin, through Amazonas, to the coast. San Martin suffers from much higher levels of wildlife trafficking than Amazonas, with active wildlife markets, and various tourist centers which keep animals illegally, and restaurants that serve bush meat (Rowe and Martinez 2003; Shanee 2012b). *L. flavicauda* individuals are rarely sold as pets since they are very sensitive to captivity and infants usually die shortly after capture (pers. obs.).

Between 2007 and 2011, 23 *L. flavicauda* individuals were extracted from the wild (Shanee 2012b). However, these data do not include information from indigenous communities where this species is heavily hunted for bush meat and traditional costumes for festivals (Shanee et al. 2007a; Leo Luna, pers. comm.; DeLuycker 2007). Migrant populations are opportunistic hunters and generally do not consume primate meat (Shanee 2012b). Nevertheless, hunting for bush meat consumption and local pet trade do take place in migrant populations. Leo Luna (1987) estimated that approximately 600 yellow-tailed woolly monkeys were hunted between the mid-1970s and the mid-1980s, causing the local extinction of several populations.

Crop Raiding

There is little information about crop raiding in neotropical primates, and it is assumed that human–wildlife conflicts are significantly less common in the neotropics than in Africa and Asia (Barnett et al. 2002; Estrada 2007). Nevertheless, it does represent a concern for local farmers since *L. flavicauda* together with *Cebus* spp. is known to consume corn among other crops (Shanee 2012b). In some cases, crop raiding leads to direct retaliation, including the killing of primates. Furthermore, with the expanding conversion of forest habitat to small-scale farms, this phenomenon is expected to increase.

Climate Change

Peru is the third country facing the highest risk of climate change hazards, and rural areas are the most vulnerable (Brooks and Adger 2003; UNFCCC 2007). Tropical montane cloud forests are considered the most susceptible tropical forest ecosystem to climate change (Markham 1998; Bubb et al. 2004; Still et al. 1999).

Researchers predict that the chain effects of climate change will further endanger *L. flavicauda*'s habitat and the species itself: a significant shift of lower altitude ecosystems upslope, consequently replacing higher altitude forests which will then be forced into extinction; reduced cloud immersion by vegetation, resulting in the drying of the ecosystem; reoccurring droughts and extreme rains; intensification of catastrophic wildfires; and alteration in plant phonologies, affecting the reproduction of plant species themselves as well as food availability to dependent fauna (Bubb et al. 2004; Chapman and Peres 2001; Corlett and Lafrankie 1998; Bawa and Dayanandan 1998). The imbalance produced by these processes could lead to famine and limit primate reproductive success (Wright 2007; Bawa and Dayanandan 1998). Consequently, montane forest endemic species, because of their restricted altitudinal ranges, are more prone to extinction (van der Hammen 2005; Foster 2001).

Although systematic precipitation and temperature studies are not available for the area, local people report severe abnormalities in the timing and severity of the dry and wet seasons, as well as heat waves, strong winds, flooding, wild fires, and drastic changes in forest phenology. The low fruit production caused by a long dry season in 2010 forced groups of *L. flavicauda* at La Esperanza to consume higher proportions of leaves and insects (pers. obs.). We also observed that the fruits of *Styloceras laurifolium,* one of the main food sources of yellow-tailed woolly monkeys, rarely matured during the period between 2009 and 2010 as frequent windstorms dislodged the fruits before they ripened.

The increasing effects of climate change and land degradation also increase pressure on farmers, as they are required to increase efforts in order to maintain the same levels of production, thus leading to more clearing, uncontrolled burning, and illegal resource use. As climate perturbations show increasing trends, they are likely to become one of the main threats to *L. flavicauda*.

Extraction Projects

Mining in Peru occurs mainly in the mineral-rich Andean Sierra (Dourojeanni et al. 2009). In many cases, this has a direct effect on yellow-tailed woolly monkey's habitat via deforestation, or, in cases when mining occurs at elevations above the species habitat, via river diversion, contamination, and/or major landslides. Figure 16.1 shows mining concessions awarded in areas which were defined by Buckingham and Shanee (2009) as *L. flavicauda* habitat. The mining situation is not static as new concessions are authorized by the Ministry of Energy and Mines annually.

There are 550 mining concessions in Amazonas and 216 in San Martin (MEM 2011). In San Martin, 36 mining concessions and 78 concession applications occur

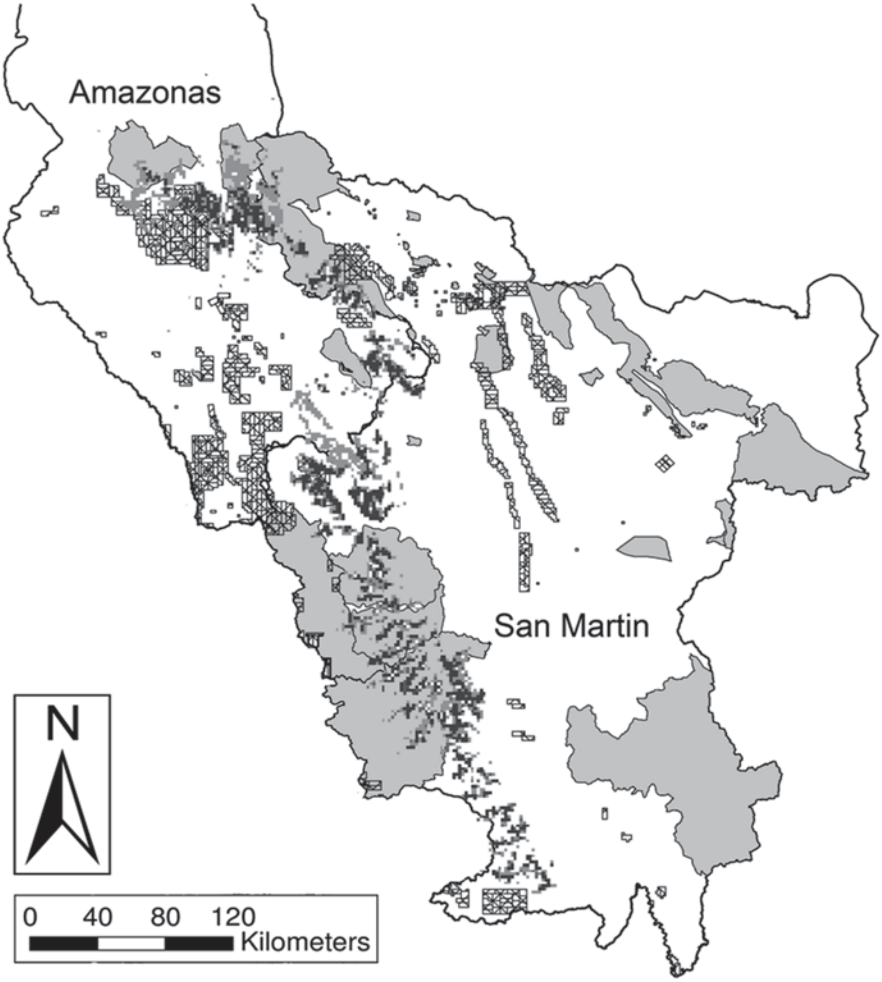

Fig. 16.1 Map showing *L. flavicauda* habitat highlighted in Buckigham and Shanee (2009) with mining concessions

within municipal, regional, national, and private reserves. There are 13 concessions and 43 applications in areas destined for protection and conservation, according to the San Martin Regional Government's territorial ordering (Pinasco Vela et al. 2009). According to Peruvian law, managers of protected areas (PAs) have the authority to stop concession holders from beginning operations within the designated limits and their buffer zones.

Most mining projects in this area are still in their early stages, so the full extent of their impact on *L. flavicauda* is hard to assess. However, legal loopholes, lack of supervision, and faulty environmental actions are common in Peru (Arellano-Yanguas 2008; Dietsche et al. 2007; Shanee 2012a). It is also clear that the contribution of these factors to land degradation will go beyond direct deforestation and pollution, since road building and subsequent attraction of a migrant work force will add to the environmental dangers (McMahon and Remy 2001).

Road Construction

Roads are a common cause of deforestation and forest degradation (Young 1994; Dourojeanni 1981; Dourojeanni et al. 2009), through intensified migratory agriculture and logging (Fearnside 1986), increased forest fires (Nepstad et al. 2001), and wildlife traffic (Peres and Terborgh 1995; Wilkie et al. 2000). Humid montane forests are especially vulnerable to the ravages of road construction, placing specialized species at great risk (Young 1994).

Studies conducted in the Upper Huallaga river basin have shown a high probability of deforestation in strips of up to 10 km on either side of roads, an effect that only diminishes when valleys are particularly steep (CDC-UNALM 2004). In lower Amazonia, deforestation can reach up to 100 km from paved highways (Laurance et al. 2001; Laurance et al. 2002). Jerozolimski and Peres (2003) found that hunting can occur anywhere within 9 km of any access point.

There are at least six major roads currently under construction within *L. flavicauda's* habitat which, if and when completed, would divide the species habitat into eight parts (Shanee 2011), further exposing it to the dangers of forest fragmentation (Marsh 2003). The Marginal Highway Fernando Belaunde Terry is the main reason for the drastic increase in human population and deforestation in the Amazonas and San Martin regions since its construction in the 1980s (Shanee 2012a).

Dozens of smaller roads are constantly solicited by rural villagers to establish a connection with the main highways, further fragmenting *L. flavicauda*'s habitat. The low budgets of regional governments slow road construction, but plans exist and are frequently revisited. Most small roads are built without valid environmental impact assessments and attract migration and further encroachment on forested lands.

Logging

L. flavicauda is able to survive in forests which are selectively logged at least in the short term (Shanee and Shanee 2011). Yet, selective logging is known to affect primate species' breeding and foraging strategies (Wilson and Wilson 1975; Isaac and Cowlishaw 2004). Additionally, studies show that even selective logging has important direct impacts on forests, such as soil erosion and compaction, vine and grass invasions, and microclimatic changes (Johns 1997), as well as indirect impacts including the opening of trails for migrant settlers and hunters (Laurance 1998; Johns 1997; Chomitz and Gray 1996).

Selective logging, usually illegal, occurs in much of the species range. With the depletion of the logged species, logging expands to more inaccessible areas, sometimes up to 2 days walk from any road.

16.2 Conservation Initiatives

Peruvian law allows the creation of different categories of PAs which can be administrated by public offices (central government, regional government, or municipalities) or private entities (NGOs, companies, associations, or individuals). Buckingham and Shanee (2009) calculated that about 30 % of the species range was officially protected, and they suggest that an urgent increase in the size and efficiency of the current PA network is necessary. Shanee (2012a) confirms that existing PAs suffer from severe economic constraints and low public participation, resulting in many infractions, thereby protecting the species populations within them only to a certain extent. Enforcement of environmental laws concerning natural resource use and land use changes is inadequate and, therefore, hunting and clear cutting continue within PAs.

16.2.1 State Initiatives

There are four national PAs containing *L. flavicauda* populations (Table 16.2).

16.2.2 Private Initiatives

Creation of Private Conservation Areas

In Peru, there are 145 privately and communally run PAs under the schemes of Private Conservation Areas, Concessions for Conservation, Ecotourism Concessions and Ecological Service Areas, totaling more than 1.5 million ha (SPDA 2013). PAs managed by the private sector have been legal in Peru since the 1990s, and their numbers have increased dramatically since the creation of the Ministry of the Environment in 2008. The increase of private initiatives is not affected by the fact that there are still no concrete benefits to initiators.[2]

Out of 29 privately owned PAs currently recognized in Amazonas and San Martin, 18 are run by local communities and associations, 3 by NGOs, and 8 by local individuals. These areas total more than 96,457 ha in Amazonas and 466,329 ha in San Martin. At least nine of these PAs protect *L. flavicauda* populations in some/all of their territory (Table 16.3). There are 16 proposals for Concessions for Conservation in San Martin waiting to be officially recognized and two in Amazonas. Several other NGOs, local communities, and associations are in different stages of their proposals.

Private and communal conservation areas supplement the national system of PAs and allow the protection of otherwise threatened forest. These areas play an

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[2] Simy Benzaquén in a meeting organized by SPDA in Chachapoyas February 2011.

Table 16.2 State-run conservation areas protecting *L. flavicauda* populations

Reserve	Category[a]	Size (hectares)	Situation
Cordillera de Colan	National sanctuary	39,215.8	Mainly protected but suffers from incursions by loggers and hunters from neighboring communities and low levels of migration of farmers (Bartra 2010)
Rio Abiseo	National park	274,520	An estimated 85,200 ha is within the altitudinal range of *L. flavicauda* (M. Leo Luna unpublished data). Threats from mining activities exist to the reserve, although this has drastically reduced in recent years. However, there are a small number of cattle ranchers in the reserve
Alto Mayo	Protected forest	182,000	Suffers from high levels of migration and forest clearance. Park management estimates 3,000 families living inside it and by 2009, 26,000 ha were deforested, equal to about 15 % of the total size of the reserve
Rio Nieva	Reserved zone	36,348.3	Currently in process of categorization. Created without prior consultation with villages inside the area and therefore suffers from high levels of negative response from local populations (Shanee 2012a)

[a] Peru has nine categories of management for PAs specified in the Protected Natural Areas Law, No. 26834, which allows different resource-use intensities according to the objectives set by the creation of a particular area

Table 16.3 Private conservation areas protecting *L. flavicauda* populations in some/all of their territory

Region	Name of reserve	Category	Size
Amazonas	Hierba Buena–Allpayacu	Private conservation area	2,282
Amazonas	Copallin	Private conservation area	11,549
Amazonas	Abra Patricia–Alto Nieva	Private conservation area	2,514
Amazonas	Alto Nieva	Conservation concession	6,700
San Martin	Alto Huyllabamba	Conservation concession	143,928
San Martin	El Breo	Conservation concession	113,826

important role in the protection of *L. flavicauda*'s habitat, especially in cases, such as the Community of Copallin (11,550 ha) and Alto Huayabamba CC (143,928 ha), which border national PAs and, thus, increase their size and preserve essential habitat connectivity (Bennett 1999). The creation and maintenance of these private PAs, especially by local people, are challenged by a very complex process which requires much collaboration with NGOs, economic resources, organization within the community, or association (Shanee et al. in press). Private PAs motivated by water preservation needs are often located in areas which are not suitable for *L. flavicauda*, and reserves for ecotourism are often located in areas which are below the species' altitudinal range. Forests with abundant fruit to sustain high densities of primates are usually a sign of good soil fertility (Peres 2008) and, thus, attractive to farming. Therefore, many private initiatives choose to conserve marginal areas for yellow-tailed woolly monkey conservation.

16.2.3 Landscape-Level Conservation

It is acknowledged that PAs, due to their small size, low numbers, and isolation, are not sufficient for species conservation and must be complemented by landscape management strategies, composed of a matrix of production and protection areas (Ancrenaz et al. 2007; Harris 1984; Margules and Pressey 2000; Newmark 1987). This is especially true for species occurring in densely inhabited and productive areas, where PAs are unfeasible and forest destruction levels are high (Ranta et al. 1998). The literature emphasizes the importance of conserving forest fragments and "seminatural" lands for the survival and dispersal of these species (Bennett 1999; Bierregaard Jr et al. 1992; Gascon et al. 1999; Hansen et al. 1991; Harris 1984; Terborgh 1992). Suggested methodologies include protection and restoration of corridors, which can be in the form of riparian forests or farm boundaries, leaving and planting native fruit trees within agriculture lands, and controlled hunting (Bennett 1999; Lyon and Horwich 1996; Margules and Pressey 2000). As *L. flavicauda* is able to survive in disturbed, mixed-use forest (Shanee and Shanee 2011; Shanee 2011), this species can potentially benefit from these types of conservation initiatives.

Throughout *L. flavicauda*'s range, there are many initiatives of local communities to reduce hunting and/or clear cutting within their jurisdiction. These communities use communal institutions, which often replace absent national authorities in the enforcement of environmental laws. The communities report trends towards forest regeneration and the return of large animals such as primates to areas where they were absent for many years (Shanee et al. in press).

The essence of landscape-level conservation is its large geographical extension, including populated areas. This approach can offer more protection for *L. flavicauda* populations. On the other hand, landscape-level conservation is mainly informal; therefore, it has little legal power against national and regional development plans, as well as against continuous in-migration to the area and its consequences.

16.3 Conclusion

Leo Luna (1980, 1982, 1987) identified hunting, selective logging, and habitat loss, resulting from agricultural expansion and road construction, as the main threats to *L. flavicauda* and predicted an increase in their negative effects over time. Indeed, all of these threats persist and have recently intensified. Moreover, new threats have also appeared.

Based on the parameters predicting extinction risks, increasing threats indicate that the species is extremely susceptible to extinction through stochastic events, inbreeding, anthropogenic pressures, and slow rates of adaptation (Lande et al. 1999; Gaston 1994). Nevertheless, *L. flavicauda*'s ability to survive in disturbed forests, at least in the short term, is a prominent factor in the species' survival and creates opportunities for conservation in anthropogenic landscapes.

The population size estimates presented here are preliminary and more studies in different habitat types, on population densities and hunting practices, are needed. However, it is clear that the species' population size and habitat are decreasing; this trend will likely increase as the threats identified here all show growing tendencies.

The most important conservation opportunity for *L. flavicauda* in the area is land conservation by the private sector, especially of local, rural communities. We suggest that the most effective conservation solution for this species is the combination of private PAs and landscape-level conservation where PAs offer better protection within smaller areas and landscape-level conservation offers partial protection over more extensive areas.

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